Volume LXXI Number 4

THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

APRIL 1921

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EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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THE
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APRIL 1921

EFFECT OF LIGHT ON GERMINATION OF LIGHT-SENSITIVE SEEDS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 279

WRIGHT A. GARDNER

Historical

Various explanations have been offered for the germination of light-sensitive seeds, and several conditions have been shown to favor or make possible the germination of such seeds. Rupture of coats, increased water supply, variation of quantity and intensity of light, reciprocal relation of heat and light, reaction of substratum and embryo, activation of enzymes, increased oxygen pressure, increased carbon dioxide pressure, and "certain inhibiting agencies" have been suggested as factors affecting the germination of light-sensitive seeds. Although quite possible, it seems hardly probable that no one of these is the fundamental or controlling factor. It would seem quite probable that one or two of these agencies are fundamental and the others are accessory means of setting in motion the processes that finally bring about germination. Enzyme action has been suggested repeatedly as a fundamental cause of germination, but no one has ventured to demonstrate the relation of enzymes to the germination of light-sensitive seeds.

An attempt has been made in this investigation to discover the fundamental relation of light to the germination of seeds, and to show just what light does to start germination. The effect of light on the germination of seeds has interested botanists for many years.

The first known publications on this subject were made by CASPARY (4) in 1860, when he announced that the seeds of *Bulliarda aquatica* are strongly light sensitive. In 1867 he (5) discussed the germination of seeds of *Pinguicula vulgaris*. In 1876 NOBBE (38) made the statement that germination was neither favored nor influenced by light. After WIESNER (51) had published the statement that the germination of seeds of *Viscum album* is favored by light, and STEBLER (48) had shown that *Poa pratensis* and *P. nemoralis* germinated up to 60 per cent in light and only up to 7 per cent in darkness, NOBBE (39) published results of experiments with grass seeds, including *Poa pratensis*, *Zea Mays*, and some other large seeds to uphold his earlier contention. PAUCHON'S (41) results supported NOBBE in the controversy. In 1883 CIESLAR (6) confirmed and extended STEBLER'S results, reporting *Agrostis stolonifera* and *Nicotiana macrophylla* as light sensitive. He made a careful study of the influence of temperature in connection with light, and showed that small seeds poor in reserve materials germinate better in white light, while large seeds are usually indifferent to light, and that seeds of *Poa nemoralis* germinate better in yellow light than in violet. LIEBENBERG (35) in 1894 confirmed STEBLER'S results, but referred to them as temperature effects.

In 1893 JÖNSSON (23) showed that after-ripening has a definite influence on the action of light in germination, that light increases the percentage of germination, that heat rays are unimportant, that intermittent light is as effective as continuous light, and that intermittent temperature may be substituted for light in the germination of such seeds as *Poa pratensis*, *P. nemoralis*, *Agrostis stolonifera*, and *Daucus Carota*.

In 1899 HEINRICHER (19) began publishing the results of his work on light germination. He (20) reported that seeds of *Pitcairnia maydifolia* germinate only in light, that the germination of *Veronica peregrina* seeds is hastened and several other small seeds are favored in germination by light. He considered the factors to be age, quickness of drying, moisture, illumination of parent plant, and light of different colors. He (21) concluded that the effect of light is a matter of activation of reserve materials, that the benefit of light is not due to its causing early carbon assimilation,

but rather to its effect on the enzyme activity in the production and digestion of stored foods. RACIBORSKI (**43**) found that tobacco seeds germinate in diffused light after 1–5 hours' illumination, a longer time being required if the intensity of light is low. In 1900 TAMMES (**49**) declared that the exposure of dry seeds to direct sunlight did not affect their later germination, and in 1902 LAURENT (**29**) made the same statement. REMER (**44**) reported that light hinders the germination of *Phacelia tanacetifolia*, but offered no explanation of the light relations. LASCHKE (**28**) confirmed earlier results with *Poa*, and stated that light cannot be replaced by higher temperatures. In the same year FIGDOR (**10**) made a report on the influence of light on the germination of seeds of Gesneriaceae. In 1912 he (**11**) reported that seeds of 12 species of this family are favored by light. In 1908 BESSEY (**3**) found that seeds of the epiphytic *Ficus aurea* and *F. populnea* germinate only in light.

KINZEL (**24**) in 1907 reported that the germination of freshly harvested seeds of *Nigella sativa* was prevented by light, while similar seed germinated up to 94 per cent in darkness. Even three minutes' illumination after 24 hours' incubation in darkness had a marked retarding effect. He considered the effect of light as photochemical, and designated such seeds as "light hard." The germination of some light-sensitive seeds in darkness was hastened by soaking in a solution of an enzyme such as papayotin (**25**). He (**26**) also published a long list of light-sensitive seeds, to which still others were added in his later work (**27**). He recognized as important factors in germination of seeds age of seed, character of seed coats, and color of light. LEHMANN'S work (**30, 31, 32, 33, 34**), begun in 1909, continued through 1915. Most of his experiments were conducted with seed of *Verbascum Thapsus*, *V. thapsiforme*, *Epilobium roseum*, and *Ranunculus sceleratus*. He showed the effects of substratum on germination in light, found the age of seeds to be an important factor, used Knop's nutrient solution as a stimulus instead of light, and found that salts favored germination of light-sensitive seeds in darkness. He claimed that light exerts its influence by starting or stopping some chemical changes in the seed, and established a relation between light and temperature. He also punctured seed coats as a substitute for light. LEHMANN

and OTTENWÄLDER (**36**) experimented with *Epilobium hirsutum* and other seeds and showed that acid solutions and proteolytic enzymes can be substituted for light. They referred the light effect to activation of enzymes, but did little to prove their hypothesis. PICKHOLTZ (**42**) connected light effects and temperature variations, and concluded that the influence of direct sunlight was mainly due to the heat rays which raised the temperature. Alternating temperatures helped the germination at different stages of maturity.

In 1912 a number of workers reported on the problem of light germination. BAAR (**1**) investigated seeds of several Amarantaceae and found that most seeds of this family (*Amaranthus*, *Celosia*, and *Blitum*) have an aversion to light. He considered the age of seeds generally important for the occurrence and intensity of the light effect, and also related the light effect to substratum and temperature variations. BECKER (**2**) brought forward a long list of examples of the light effect on germination of seeds. HAACK (**18**) in his work on the Scotch pines demonstrated the influence of heat, and reported that temperature variations act as a stimulus to light-sensitive seeds, and that blue light is more favorable to germination than darkness. SIMON (**47**) reported that the salts of iron hindered germination of seeds in darkness, but increased it in light. GASSNER (**12**) first reported on the germination of seeds of *Chloris ciliata* in 1910. He found three factors which may be substituted for light, namely, increased oxygen supply, after-ripening, and high temperature. He claimed that light offsets the effect of the limiting factor, and showed that the chaff of *Chloris ciliata* prevents easy germination. His later work (**14, 15**) took up the action of chemicals. He considered the latent influence of light as related to seed bed, temperature, and after-ripening, the influence of light on germination, the influence of desiccation, and the relations between light and media favoring or hindering germination. From a tabulation of tests with seeds of different families he concluded that in these cases nitrogen, variously combined in the media, shows the same favorable action as light, but he included contradictory results. He considered the favorable effect of Knop's nutrient solution as due only to the nitrates present. He reported the seeds

of *Ranunculus sceleratus* and *Oenothera biennis* as favorably influenced by light and by inorganic salts containing nitrogen, through a wide range of concentrations. OTTENWÄLDER (40), working with *Epilobium hirsutum* seeds, found that the light requirement as regards intensity is closely related to temperature, the former increasing as the latter is lowered. The illumination period is related also to the temperature, but more closely to light intensity. Light-sensitive seeds are also favorably and strongly influenced by weak acids. The hypothesis of a catalytic influence of light is said to have received support from these observations.

Materials

A preliminary examination of 115 samples of seeds collected from Shaw's Gardens, the Botanical Gardens of the University of Michigan, waysides, swamps, and fields indicated the following as available for the study of the effect of light in germination: *Daucus Carota*, *Nicotiana Tabacum*, *N. sylvestris*, *N. affinis*, *Nicotiana* hybrids, *Gentiana Saponaria*, *G. pannonica*, *Oenothera biennis*, *Verbascum Thapsus*, *Amaranthus caudatus*, *Rumex crispus*, *Phoradendron flavescens*, and *Datura Stramonium*. Of those mentioned, the writer has been unable to find any previous report of light sensitiveness of seeds of *Rumex crispus*, *Datura Stramonium*, and *Phoradendron flavescens*. Of the light-sensitive seeds not previously reported, seeds of *Rumex crispus* and *Phoradendron flavescens* are favored by light in germination, while seeds of *Datura Stramonium* are inhibited from germinating by light, as will be shown later.

JÖNSSON (23) in 1893 reported the seed of *Daucus Carota* as favored by light in germination. *Nicotiana Tabacum* seeds were first reported as light sensitive by RACIBORSKI (43) in 1900. The seeds of *Gentiana Saponaria*, *G. pannonica*, *Verbascum Thapsus*, and *Oenothera biennis* were reported as light sensitive by KINZEL (24) in 1907. BAAR (1) reported *Amaranthus caudatus* seeds as hindered in germination by light. The seeds of *Gentiana* are not conveniently suited to the purposes of this investigation on account of the longer incubation period. The seed of *Amaranthus caudatus* are not used because they are light-inhibited seeds. The seeds

of *Datura Stramonium* have been found by careful experiments to be light inhibited and to require total darkness and a temperature of about 30° C. for germination. They are accordingly reserved for a future study. Detailed study of the germination of *Phoradendron flavescens* seeds was deferred on account of the peculiar slimy ovary and the chlorophyll-bearing embryo. Seeds of *Nicotiana Tabacum*, *Rumex crispus*, *Oenothera biennis*, *Verbascum Thapsus*, and *Daucus Carota* were selected for this research because of their abundance and similar incubation periods.

Germination in light and darkness

Preliminary tests of *Rumex crispus* seeds on wet filter paper gave a germination of 84 per cent in light and 16 per cent in darkness after 8 days of incubation.

TABLE I

Treatment	Percentage germination in light	Percentage germination in darkness
Cleaned, dried, and soaked in flowing water for 24 hours and incubated	16	6
Cleaned, dried, and incubated	24	6
Cleaned, soaked for 4 days, and incubated	12	2

Preliminary tests of germination of seeds of *Phoradendron flavescens*, suggested by WIESNER'S (**51**) results with seeds of *Viscum album*, are given in table I. Seeds prepared as indicated in table I were counted into Petri dishes containing wet filter paper as substratum and placed in light and total darkness to incubate at room temperature, which ranged from 18–25° C. The incubation period was 27 days. These results indicate that light favors the germination of seeds of *Phoradendron flavescens*. On account of the sticky nature of the pulpy ovary and the succulence of the single fleshy green embryo, it was almost impossible to remove the mass of enveloping material without leaving a favorable substratum for molds and bacteria on the one hand, and without injury to the embryo on the other hand. Moreover, with the best of care many of the seeds failed to germinate and became moldy. With these

conditions we can understand the relatively low germination, and yet see that light favors the germination of these seeds.

Seeds of *Datura Stramonium* were treated as shown in table II. Seeds were allowed to incubate for 17 days, and the results indicate clearly an inhibitory action of light on their germination. The

TABLE II

Treatment	Percentage germination in light	Percentage germination in darkness
On soil, 26–30° C	6	98
On sand, 26–30° C	2	22
On filter paper, 20° C.	0	0
On filter paper, 24° C.	0	4
On filter paper, 30° C.	4	60

constituents of the soil solution seem to promote materially the germination of these seeds in darkness but not in light. *Datura Stramonium* seeds require different treatment from any of the other seeds tested, and accordingly are reserved for separate study.

Light sensitiveness, after-ripening, and viability

To establish standards for comparison with other data, and to indicate the degree of light sensitiveness, various light-sensitive seeds were incubated from time to time at room temperature (20–28° C.) on filter paper in light and darkness respectively. The results given in table III are fairly representative of these tests.

These data indicate what may be expected of the various light-sensitive seeds under investigation when subjected to germinating conditions at room temperature 20–28° C. on wet filter paper in Petri dishes. It appears that the seeds of some kinds of tobacco are less light favored than others (3. *Nicotiana affinis*, 108. *N. affinis*, 1. *Nicotiana* hybrid, and 117. Pennsylvania Havana tobacco). The results also indicate that not all of the seeds under investigation are entirely dependent on light for germination. A certain percentage of each lot of *Rumex crispus* and *Daucus Carota* seeds usually germinates in darkness. It is also noteworthy that seeds of *Oenothera biennis* do not always germinate, even in light. The seeds under investigation seem to retain their light sensitiveness

for long periods and to a rather high degree, especially those of *Verbascum Thapsus* and *Nicotiana Tabacum*. Attention should be called to low germination of newly harvested seeds of *Oenothera biennis*, *Daucus Carota*, and *Rumex crispus*. Tests for evidence of

TABLE III

Seeds	Incubated 9–18–15 to 9–29–15		Incubated 10–28–15 to 11–5–15		Incubated 5–30–16 to 6–6–16		Incubated 6–20–18 to 6–28–18	
	Light	Darkness	Light	Darkness	Light	Darkness	Light	Darkness
	Collected in 1914							
1. Nicotiana hybrid	91	56	87	65	87	60	84	45
3. Nicotiana affinis	79	57	87	45	74	43	82	19
8. Nicotiana hybrid	48	1	58	5	74	35	67	13
13. Nicotiana hybrid	84	0	89	2	89	6	80	0
22. Nicotiana hybrid	55	0	73	0	61	0	55	0
55. Verbascum Thapsus	81	1	80	0	87	0	53	0
61. Daucus Carota	63	19	78	10	71	20	32	7
66. Oenothera biennis	4	2	76	10	51	4	0	0
68. Rumex crispus	39	8	88	18	75	31	60	1
92. Nicotiana Tabacum	77	1	.....	.....	90	4	30	0
96. Daucus Carota	1	0	52	6	.....	.....	.....	.....
	Collected in 1915							
97. Verbascum Thapsus	94	0	94	0	82	0	.....	.....
98. Oenothera biennis	2	0	48	0	61	1	.....	.....
99. Rumex crispus	36	0	82	4	80	40	66	0
100. Verbascum Thapsus	74	1	73	0	39	0	60	0
101. Rumex crispus	61	0	94	0	92	2	30	0
102. Daucus Carota	.....	.....	45	1	44	11	.....	.....
103. Oenothera biennis	.....	.....	63	0	61	0	.....	.....
104. Rumex crispus	.....	.....	94	1	79	11	.....	.....
105. Pennsylvania seedleaf tobacco	.....	.....	.....	.....	75	24	.....	.....
111. Connecticut seedleaf tobacco	.....	.....	.....	.....	75	0	.....	.....
112. Honduras tobacco	.....	.....	.....	.....	49	0	.....	.....
113. Cuban tobacco	.....	.....	.....	.....	81	0	.....	.....
117. Pennsylvania Havana tobacco	.....	.....	.....	.....	100	71	.....	.....
118. Ohio seedleaf tobacco	.....	.....	.....	.....	86	2	.....	.....

a period of after-ripening in *Verbascum Thapsus* were quite negative. Newly harvested seeds of *V. Thapsus* germinate above 90 per cent in light and only about 2 per cent in darkness. Tests of still older seeds indicate that they retain light sensitiveness as long as they are viable.

Mechanical rupture

In 1906 CROCKER (7) succeeded in germinating a number of different kinds of seeds after breaking the seed coats. KINZEL (24) found that puncturing coats of some of his light sensitive seeds gave better germination in darkness. GASSNER (13) found that rupture of the coats of seeds of *Chloris ciliata* permitted good germination in darkness at 34° C. Thus it seemed quite possible that the seeds under investigation might be brought to germination by such treatment. Accordingly a more carefully controlled experiment was made to determine the rôle of the several seed coats in germination. Seeds of each kind were rubbed on fine sandpaper and placed on moist filter paper in Petri dishes. The Petri dishes were carefully wrapped in black cloth and placed in a dark room at 24–30° C. for 8 days. Concurrently, sets of unabraded seeds were placed to germinate in light and darkness.

TABLE IV

SEEDS	NOT ABRADED		ABRADED	NOT ABRADED
	Light	Darkness	Darkness	Darkness
Nicotiana Tabacum	60, 61	0, 0	0, 1	0, 1
Rumex crispus	30, 16	0, 1	40, 66*	0, ..
Verbascum Thapsus	75, 32	0, 8	6, ..	1, 3
Oenothera biennis	10, 39	3, 0	3, 5	7, 1
Daucus Carota	60, 20	27, 7	25, 15	21, 17

* Coats off.

Mechanical abrasion of seed coats for various periods in rotating cylinders containing coarse quartz sand gave similar results. An examination of the data in table IV reveals the beneficial effect of abrasion of seed coats in but one instance. In the case of *Rumex crispus* abrasion of the seed coats yielded a percentage of germination slightly exceeding that for light in the control, while the removal of the coats yields a percentage of germination even more than double that in light. This suggests that the seed coats of *Rumex crispus* inhibit or retard the entrance of some necessary factor, or perhaps retard the exit of some inhibiting factor, and that light in some way favors these movements.

Rupture by sulphuric acid

As long ago as 1896 ROSTRUP (**45**) of the Danish Seed Control found that concentrated sulphuric acid treatment hastened germination of hard seeds of *Lathyrus sylvestris*. TODARO (**50**) used concentrated sulphuric acid on red clover seed with beneficial results. He also reported that various weed seeds, including those of *Rumex crispus*, were all destroyed by a brief immersion in sulphuric acid. Accordingly, to determine more certainly the rôle of seed coats in the germination of the five kinds of seeds, they were treated with concentrated sulphuric acid for periods previously determined, carefully washed in carbonate of soda solution, then in distilled water, and placed in germinators as previously described.

TABLE V

SEEDS	TREATED WITH CONCENTRATED SULPHURIC ACID				UNTREATED	
	Minutes in H_2SO_4	Germinated in darkness			In light 8 days	In darkness 8 days
		8 days (1)	10 days (2)	8 days (3)		
Nicotiana Tabacum.....	0.5	0	0	0	42	0
Nicotiana Tabacum.....	1	0	0	0	42	0
Verbascum Thapsus.....	0.5	0	0	0	72	0
Verbascum Thapsus.....	1	0	0	0	72	0
Daucus Carota.....	0.5	23	8	0	31	25
Daucus Carota.....	1	1	6	0	31	25
Rumex crispus.....	6	27	37	17	88	0
Rumex crispus.....	8	62	59	0	88	0
Oenothera biennis.....	8	38	34	41	78	0
Oenothera biennis.....	10	1	19	23	78	0

Table V indicates that treatment of seeds of *Rumex crispus* and *Oenothera biennis* with concentrated sulphuric acid yields an increased percentage of germination in darkness. Treatment with concentrated sulphuric acid for longer or shorter periods than indicated gives no better germination of the seeds in darkness. In *Daucus Carota* there is apparently an injury. This experiment indicates that light acts on the coat of *Rumex crispus* seeds, and points in that direction in case of seed coats of *Oenothera biennis*. These results in the main agree with those of the experiment on abrasion of coats. They confirm the results with seeds of *Rumex*

crispus and include the seeds of *Oenothera biennis* as being benefited in germination by acid treatment. Why the seeds of *Oenothera biennis* germinate better after treatment with H_2SO_4 and not by abrasion is unexplained.

Temperature and light

OTTENWÄLDER (40) claimed that within the range of temperatures which permit germination, light can be substituted for heat at low temperatures and heat for light at high temperatures. With *Verbascum Thapsus* and other seeds he found that germination occurred at high temperature in darkness and at low temperature

TABLE VI

Seeds	Temperature centigrade							
	10°	15°	19°	24°	27°	30°	35°	40°
	Light							
Nicotiana Tabacum	0	0	23	62	55	40	.....	.....
Verbascum Thapsus	0	0	0	77	82	84	.....	.....
Daucus Carota	0	12	21	36	33	25	.....	.....
Oenothera biennis	0	0	0	28	.....	6	.....	.....
Rumex crispus	0	1	42	65	22	5	.....	.....
	Darkness							
Nicotiana Tabacum	0	0	0	11	6	2	0	0
Verbascum Thapsus	0	0	0	7	14	15	3	1
Daucus Carota	0	4	7	16	12	12	4	0
Oenothera biennis	0	0	0	5	4	2	0	0
Rumex crispus	0	1	3	8	8	4	0	0

in light. In order to test this for American *Verbascum Thapsus* and to see whether it is generally true, the different seeds under investigation were placed to germinate in light and darkness at different temperatures. It was not possible to control closely temperature and prevent small fluctuations. These changes of temperature were never sudden, however, and had no effect except to increase slightly the percentage of germination in both light and darkness. The data reported represent results obtained from five different sets of determinations. Seeds were placed to germinate in Petri dishes on filter paper wetted with distilled water at temperatures indicated in table VI and allowed to incubate for 9 days.

These data offer no evidence of a reciprocal relation between heat and light as suggested by LEHMANN and OTTENWÄLDER, not even in the case of seeds of *Verbascum Thapsus*, nor have any of the various tests indicated this reciprocal relation in the seeds. Indeed, in each kind of seed under investigation the optimum temperature for germination in light is very close to that for germination in darkness. In germination in darkness the results show rather definite minimum and maximum as well as optimum temperatures. It is especially noteworthy that high temperature and darkness did not induce germination of *Verbascum Thapsus* seeds, as claimed by OTTENWÄLDER (**40**). No specific experiments were performed to determine the effect of light intensity on germination, although early in this investigation it became a very familiar fact that very little illumination would induce germination. Good germination in darkness was frequently the occasion for repetition of an experiment, only to find that germination had been induced by leaks in the light screens. A comparison of table VI with data given elsewhere indicates that highest germination of light-sensitive seeds does not occur at constant temperature, but at temperatures fluctuating between 20 and 27° C.

Effects of alternation of temperature, light, and darkness

As long ago as 1882 NOBBE (**39**) and his students used alternating temperatures to promote germination, and in 1884 LIEBENBERG (**35**) referred light effects to variations of temperature in the germination of seeds of *Poa pratensis*. As recently as 1911 PICKHOLTZ (**42**) referred the action of light in promoting germination to the effects of heat rays. In an attempt to distinguish the effects of light from those of temperature the following experiments were performed. Seeds of each kind were counted into Petri dishes with filter paper wetted with distilled water as substratum. One lot of cultures was placed in darkness on February 9 at 40° C., where it remained for 17 days. Another lot of cultures was placed in darkness at temperatures ranging from 0 to 12° C. for 17 days. Another lot was kept in darkness and subjected alternately to high temperature (40° C.) and low temperature (0–12° C.) for nearly equal periods throughout the 17 days. The low temperature and the

alternating temperature cultures were frozen on the morning of February 26. On this date observations were made and the cultures placed in light at room temperature to test viability.

As shown in table VII, the constant high temperature effectively inhibited the germination of all seeds except those of *Verbascum Thapsus*. The subsequent incubation in light at room temperature showed fatal injury to the embryos of *Daucus Carota*, *Oenothera biennis*, and *Nicotiana Tabacum*. The constant low temperature delayed germination, but seemed to induce increased germination in light in seeds of *Daucus Carota*, *Oenothera biennis*, and *Verbascum Thapsus*. This is especially noticeable in *Oenothera biennis* seeds.

TABLE VII

Seeds	Constantly at 40° C. in darkness for 17 days (*a*) and then at room temperature in light for 12 days (*b*)		Constantly at 0–12° C. in darkness for 17 days (*a*) and then at room temperature in light for 12 days (*b*)		Alternately at 40 and 0–12° C. in darkness for 17 days (*a*) and then at room temperature in light for 12 days (*b*)		Control at room temperature for 11 days	
	(*a*)	(*b*)	(*a*)	(*b*)	(*a*)	(*b*)	Light	Darkness
Verbascum Thapsus	14	78	0	86	6	90	76	2
Rumex crispus	0	54	0	58	0	56	82	30
Daucus Carota	0	1	0	60	0	8	32	6
Oenothera biennis	0	4	0	64	0	90	14	0
Nicotiana Tabacum	0	0	0	40	0	26	58	0

The alternating high and low temperature treatment delayed the germination in the same way as did constant low temperature. As shown by the subsequent incubation, *Daucus Carota* seeds were injured most. The germination of seeds of *Nicotiana Tabacum* and *Rumex crispus* was materially reduced by this treatment, while the germination of seeds of *Verbascum Thapsus* was favored, and the germination of seeds of *Oenothera biennis* very greatly increased.

In a further effort to distinguish effects of light and temperature an experiment was carried out as follows. Seeds were counted into Petri dishes, having filter paper wetted with distilled water for substratum, and placed under the following conditions: set *a* in light at 10° C. for 8 days and then at 25° C. for 8 days; set *b* in darkness at 10° C. for 8 days and then at 25° C. for 8 days; set *c*

in light at 10° C. for 8 days and then in darkness at 25° C. for 8 days; set *d* in darkness at 10° C. for 8 days, then at 40° C. for 4 days, followed by 4 days at 25° C. At the end of the 16 days' treatment all of the cultures were placed in light for 8 days at room temperature. The experiment was begun July 24.

Comparison of the data in *a* of table VIII with the control indicates that incubation in light at low temperature followed by incubation at room temperature results in reduction of percentage of germination of *Daucus Carota* seed. A comparison of *a* and the control indicates that alternating temperatures may in a measure replace light in the case of germination of *Verbascum*

TABLE VIII

Seeds	Constantly at 25° C. for 24 days		(a)			(b)			(c)			(d)		
	Light	Darkness	In light at 10° C. for 8 days	Then at 25° C. for 8 days	Then at 25° C. for 8 days	In darkness at 10° C. for 8 days	Then at 25° C. for 8 days	Then in light at 25° C. for 8 days	In light at 10° C. for 8 days	Then in darkness at 25° C. for 8 days	Then in light at 25° C. for 8 days	In darkness at 10° C. for 8 days	Then at 40° C. for 4 days, then at 25° C. for 4 days	Then at 25° C. in light for 8 days
Verbascum Thapsus	94	0	0	95	98	0	64	83	0	71	71	0	1	88
Rumex crispus	89	2	0	98	98	0	2	63	0	94	97	0	31	34
Daucus Carota	60	4	0	14	15	0	2	16	0	11	11	0	13	13
Oenothera biennis	85	0	0	69	69	0	16	16	0	2	2	0	4	12
Nicotiana Tabacum	53	0	0	70	72	0	0	3	0	35	35	0	0	1

Thapsus seeds, that it is an important factor in the germination of *Rumex crispus* seeds, and further indicates the necessity of light in the early periods of incubation of *Daucus Carota*, *Oenothera biennis*, and *Nicotiana Tabacum*. A comparison of *b* with *a* points again to the necessity of light in *Rumex crispus*, *Daucus Carota*, *Oenothera biennis*, and *Nicotiana Tabacum*, and indicates that some inhibiting factor developed during the 8 days in darkness in the case of *Oenothera biennis* and *Nicotiana Tabacum*. A comparison of *c* with the control indicates that light does its work on such seeds as *Verbascum Thapsus*, *Rumex crispus*, and in a measure on *Nicotiana Tabacum* even at low temperature, and that as soon as heat is supplied germination occurs. Incubating *Daucus Carota* and *Oenothera biennis* seeds at low temperature for a period of 8

days, in light or darkness, produces a condition from which they do not recover when incubated at 25° C. in light or in darkness. A comparison of *d* with control *a*, *b*, and *c* indicates that sudden changes from extremes of temperature may delay germination of *Verbascum Thapsus* seeds, that such treatment inhibits the germination of a large percentage of *Rumex crispus* seeds, and that it almost entirely inhibits the germination of seeds of *Nicotiana Tabacum*. The results in *d* confirm the observations on *Daucus Carota* and *Oenothera biennis* made in connection with *b*, namely, that some limiting factor develops during incubation in darkness at low temperature which is not easily overcome. The most noteworthy result of this treatment is the complete inhibition of germination of seeds of *Nicotiana Tabacum*. This is in agreement with that found in *b*. Together these results when compared with the control indicate a light requirement for *Nicotiana Tabacum* seeds which is not replaced by any temperature combination tried.

To summarize, this experiment shows that alternating temperature may replace light in germination of *Verbascum Thapsus* seeds, that light is necessary for optimum germination of entire seeds of *Rumex crispus*, although change of temperature in a measure replaces light. The results of this experiment indicate that seeds of *Oenothera biennis* and *Daucus Carota* require light and medium temperature for optimum germination, and that incubation at low temperature in darkness permits a change which is not overcome by transfer to high temperature in darkness. Moreover, in *Daucus Carota* exposures to light at 25° C. did not bring about germination of these changed seeds. Incubation of *Nicotiana Tabacum* in darkness at 10° C. did not result in increased percentage of germination in darkness. Incubation of *Ncotiana Tabacum* seeds in light at 10° C. promoted subsequent germination in darkness.

Hot water treatment

In a further attempt to induce germination in darkness, an adaptation of the warm bath method of MOLISCH (**37**) was employed. The seeds were counted, wrapped in filter paper, inclosed in little bags of cheesecloth, and plunged into hot distilled water for 0.25 minute and 0.5 minute respectively. Great care

was taken to plunge them promptly into cold distilled water, when the hot water was squeezed out. The seeds were then placed to germinate for 7 days at room temperature under the usual conditions. Table IX indicates what may be expected of hot water treatment of seeds. Treatment at lower temperatures was ineffective and so was not tabulated. The experiment was begun March 4.

The results of the warm bath treatment are mostly negative. The percentage of germination of *Rumex crispus* in darkness is

TABLE IX

Seeds	Time (in minutes) in hot water	Treatment at 90° C.; germination at room temperature for 7 days		Treatment at 75° C.; germination at room temperature for 7 days		Treatment at 60° C.; germination at room temperature for 7 days		Untreated; germination at room temperature for 7 days	
		Light	Darkness	Light	Darkness	Light	Darkness	Light	Darkness
NicotianaTabacum	0.25	4	2	0	0	42	11	62	2
NicotianaTabacum	0.5	0	0	0	0	50	34	.....	.....
Daucus Carota...	0.25	22	0	24	6	20	3	52	2
Daucus Carota...	0.5	22	0	36	8	40	8	.....	.....
VerbascumThapsus	0.25	0	0	75	10	67	20	78	0
VerbascumThapsus	0.5	0	0	75	8	65	15	.....	.....
Oenothera biennis.	0.25	70	22	76	20	40	8	50	6
Oenothera biennis.	0.5	0	6	80	48	28	20	.....	.....
Rumex crispus....	0.25	68	40	34	12	58	35	66	18
Rumex crispus....	0.5	66	36	58	10	86	28	.....	.....

increased somewhat by treatment with hot water at 90° C., while that of *Oenothera biennis* is increased somewhat by treatment with hot water at 75° C. and 90° C. These results indicate the coat as the limiting factor in their germination. Treatment at 100° C. for short periods might furnish interesting information.

Water absorption

To determine the relation of water absorption to germination in light and darkness, 2 to 3 gm. of each of the different kinds of seeds were weighed separately and placed under favorable conditions for germination. As soon as the first germination in light was observed, the seeds were dried rapidly and weighed carefully, and the percentage of water absorbed was computed on the dry

weight basis. To confirm the results obtained a second series was treated similarly. Failing to obtain concordant results, two additional series of determinations were made. The variation in time of the appearance of the first hypocotyls and the uneven surfaces of the seed coats account for much of the variation in the amount of water absorbed. The results are given in table X.

In view of the small size of the seeds, their irregular surfaces, the difficulty of uniform drying, and the increase of weight on account of germination, the data of these determinations are not

TABLE X

Seeds	Series 1		Series 2		Series 3		Series 4	
	Percentage of imbibed water	No. of sprouts	Percentage of imbibed water	No. of sprouts	Percentage of imbibed water	No. of sprouts	Percentage of imbibed water	No. of sprouts
	Light							
Nicotiana Tabacum	92.9	13	82.3	10	108.5	3	65.5	8
Verbascum Thapsus	93.3	12	58.8	2	199.0	25	93.3	6
Daucus Carota	114.5	2	92.4	4	85.7	4	64.8	3
Oenothera biennis	40.7	1	48.5	4	61.7	7	39.4	11
Rumex crispus	48.4	3	43.4	2	54.3	5	52.7	29
	Darkness							
Nicotiana Tabacum	60.0	0	50.0	0	67.7	1	63.6	0
Verbascum Thapsus	81.2	0	68.0	0	90.0	2	76.9	0
Daucus Carota	90.7	0	46.1	1	97.3	1	64.0	6
Oenothera biennis	45.1	0	108.5	1	49.4	1	49.9	11
Rumex crispus	53.1	8	52.4	1	48.9	1	45.8	10

surprisingly discordant. In some cases the high percentages of water absorbed is accounted for by the many and large seedlings which could not be removed without more seriously changing the data. After eliminating the cases open to suspicion on account of the numerous sprouts, imperfect drying, etc., there appears to be relatively little difference in the percentage of moisture absorbed by seeds germinated in light and darkness. In *Nicotiana Tabacum* seeds of series 4 the imbibition is 65.5 per cent with 8 sprouts in light, while in series 3 the imbibition is 67.7 per cent with one sprout in darkness, from which it appears that germination may occur even though a smaller percentage of water is absorbed. A

comparison of determinations of absorption by *Verbascum Thapsus* seeds in light (series 2) and in darkness (series 4) indicates the same general relations. The data for the other seeds show similar results. From this experiment it appears that light is not necessary for the absorption of sufficient water for germination.

Injection of seeds with water

DE VRIES (**8**), having abandoned variation of temperatures, high temperatures (40–50° C.), and other treatments of seeds of *Oenothera biennis* as means of securing complete germination, injected soaked seeds with water under pressure of 6–8 atmospheres, after which he frequently secured germination of 100 per cent. The

TABLE XI

Seeds	Darkness for 17 days	Then in light for 7 days	Darkness for 15 days	Then in light for 7 days	Untreated	
	(*a*)		(*b*)		Light	Darkness
Verbascum Thapsus	1	4	0	24	81	0
Daucus Carota	6	10	8	12	61	21
Oenothera biennis	8	43	5	55	33	8
Rumex crispus	5	8	11	56	71	31
Nicotiana Tabacum	4	54	5	60	83	0

seeds (table XI, *a*) accordingly were soaked overnight at a temperature of 25–28° C., wrapped in filter paper, placed in water, exhausted of the air in their intercellular spaces by reducing the atmospheric pressure to 20 mm. for 1 hour, and then subjected to hydrogen gas pressure of 575–675 pounds per square inch for 24 hours. The seeds were then placed to germinate in darkness under the usual conditions. A second lot (*b*) was treated in the same way except that it was subjected to a pressure of 500–650 pounds per square inch for 48 hours. Both lots were germinated at room temperature. Evidently injection with water does not increase the germination of seeds of *Oenothera biennis*, *Nicotiana Tabacum*, *Daucus Carota*, or *Rumex crispus* in darkness. When the seeds are subsequently exposed to light, they germinate in one or both tests. These results confirm the conclusion arrived at in the weighing experiments, that impermeability to water is not the limiting factor in light germi-

nation. Perhaps better illumination of the injected *Oenothera biennis* seeds made possible the increased germination reported by DE VRIES.

Increased oxygen supply

In his investigation of the delayed germination of seeds of *Xanthium*, CROCKER (7) found that the seed coat excludes oxygen, while SHULL (46) found a very definite relation between the oxygen supply and the percentage of germination in seeds of *Xanthium*. In order to discover if increased oxygen supply would promote the germination of the light-sensitive seeds in darkness, the following experiment was performed. Counted seeds were placed on wet filter paper in open dishes and placed under water-sealed glass cylinders containing 40, 50, 60, 70, and 80 per cent oxygen respectively (table XII). Each cylinder was placed in a dark room at 23–28° C. and covered with a light-tight metallic cylinder.

TABLE XII

Seeds	Percentage of germination in oxygen				
	40	50	60	70	80
Nicotiana Tabacum	0	0	0	0	0
Verbascum Thapsus	0	0	0	0	0
Daucus Carota	3	3	9	15	24
Oenothera biennis	.....	1	1	1	3
Rumex crispus	8	.....	19	18	23

A comparison of the germination in darkness in the presence of different percentages of oxygen shows an increase of germination of seeds of *Daucus Carota* and *Rumex crispus* with an increase of oxygen supply. Other conditions in each of the cylinders being the same so far as known, this must be attributed to increased oxygen supply. A similar experiment with higher and lower percentages of oxygen would have been interesting, especially a test of germination in 20 per cent oxygen (ordinary air) under these conditions. It would probably have given results similar to those in 40 per cent oxygen and would have been rather more conclusive. The regularity of the increased percentage of germination, however, due to increased concentration of oxygen, indicates the reliability of the results. Clearly this experiment does not indicate an oxygen

deficiency in seeds of *Nicotiana Tabacum*, *Verbascum Thapsus*, and *Oenothera biennis*.

Substrata

LEHMANN (30) reported increased germination in darkness of light-sensitive seeds such as *Ranunculus sceleratus* with soil as substratum. BAAR (1) obtained an increased percentage of germination of seeds of *Amaranthus* when he substituted earth for filter paper as a substratum, but OTTENWÄLDER (40), who used soil and sand as well as filter paper as substrata for his *Epilobium hirsutum* seeds, found beneficial results in his experiments with only one lot of sand. Investigation showed that the sand had been treated with acid which had not been thoroughly washed out.

TABLE XIII

PERCENTAGE OF GERMINATION AFTER 18 DAYS

SEEDS	ON SOIL		ON SAND		IN SOIL	IN SAND	ON FILTER PAPER	
	Light	Darkness	Light	Darkness	Light	Light	Light	Darkness
Verbascum Thapsus	40	34	30	20	2	24	41	3
Daucus Carota	56	28	54	28	32	58	63	19
Oenothera biennis	2	0	2	2	0	6	3	2
Rumex crispus	68	2	46	10	12	38	42	8
Nicotiana Tabacum	70	6	78	0	56	76	71	1

In view of the divergent results with the different seeds, it was deemed desirable to determine the relation of sand and soil to germination in darkness of these light-sensitive seeds. Also the question arose as to whether light was as necessary under natural conditions as under laboratory conditions for the germination of light-sensitive seeds. The substrata were carefully sterilized, uniformly wetted, and prepared for the seeds. The seeds in "sand" and in "soil" were buried to a depth of 0.25 inch. All were put under the same temperature conditions (23–26° C.). The results are shown in table XIII. The experiment was begun May 13 and closed June 1.

The germination of seeds of *Verbascum Thapsus* on soil and sand in darkness is somewhat higher than that on filter paper. The substratum appears to have exerted a slightly favorable effect on the germination of seeds of *Daucus Carota*, but none on the other

seeds. Such results suggest a beneficial effect on some particular constituent contained only in seeds of *Verbascum Thapsus*. In light the percentage of germination seems to correspond roughly to the light intensity. Where the lighting is good, as on the filter paper or sand, the germination is good. Where it is diminished, as in the case of seeds buried in sand or soil, the germination is reduced. The increase of germination of seeds on sand or soil in darkness may be referred largely to the action of constituents of the soil and sand. The low germination of seeds of *Oenothera biennis* may be due to periodicity in dormancy, since seeds from the same lot gave a germination of 78 per cent in light and 0 per cent in darkness in October. From these results it appears that constituents of soil may only partially substitute for light with some seeds and not at all with others.

Effects of electrolytes

The effects of electrolytes on the germination of light-sensitive seeds have been variously reported. Beneficial effects on germination in darkness of *Ranunculus sceleratus* from hot water extracts of soils, Knop's nutrient solution, and salt solutions have been reported by LEHMANN (**30**). He reported no benefit from cold water extracts of soils. LEHMANN and OTTENWÄLDER (**36**) found that weak acid solutions promote germination in darkness of seeds of *Verbascum Thapsus*, *V. thapsiforme*, and *Lythrum Salicaria*. OTTENWÄLDER (**40**) reported that acids promote the germination of seeds of *Epilobium hirsutum* in darkness. GASSNER (**15**) reported that nitrogen compounds such as nitrates, nitrites, and ammonium salts through a wide range of concentrations favor the germination of seeds of *Chloris ciliata* in darkness. As many of the electrolytes reported by these investigators belonged to the lyophobe or lyophile series, a systematic study of their effects was undertaken, to discover, if possible, some relation between electrolytes and germination. Lots of 100 seeds each were counted into test tubes, about 2 cc. of a solution of an electrolyte added, and the tubes placed in darkness. After 24 hours most of the solution was drained from each test tube, which was promptly returned to the dark chamber for the seeds to germinate. The period allowed for germination was 7 days after soaking. The results are given in table XIV.

TABLE XIV

GERMINATION IN DARKNESS IN VARIOUS CONCENTRATIONS

SEEDS	N	0.1 N	0.01 N	0.001 N	0.0001 N	0.00001 N
Acetic acid						
Verbascum Thapsus	0	0	77	79	86	....
Rumex crispus	0	0	29	23	0	....
Daucus Carota	0	0	1	3	4	....
Oenothera biennis	0	8	48	42	53	....
Nicotiana Tabacum	0	0	27	46	23	....
Butyric acid						
Verbascum Thapsus	0	0	0	80	86	....
Rumex crispus	0	0	0	6	2	....
Daucus Carota	0	0	0	1	6	....
Oenothera biennis	0	0	0	45	50	....
Nicotiana Tabacum	0	0	0	38	10	....
Citric acid						
Verbascum Thapsus	....	0	40	95	98	....
Rumex crispus	....	6	11	8	13	....
Daucus Carota	....	0	10	5	12	....
Oenothera biennis	....	38	61	52	68	....
Nicotiana Tabacum	....	36	35	54	58	....
Tartaric acid						
Verbascum Thapsus	....	0	14	81	53	....
Rumex crispus	....	7	7	10	0	....
Daucus Carota	....	1	0	13	8	....
Oenothera biennis	....	2	52	75	67	....
Nicotiana Tabacum	....	21	59	50	27	....
Malic acid						
Verbascum Thapsus	....	5	64	100	91	....
Rumex crispus	....	1	22	13	6	....
Daucus Carota	....	0	3	7	1	....
Oenothera biennis	....	27	55	54	60	....
Nicotiana Tabacum	....	40	43	31	83	....
Potassium sulphocyanate						
Verbascum Thapsus	....	....	80	75	88	....
Rumex crispus	....	....	0	2	2	....
Daucus Carota	....	....	8	4	2	....
Oenothera biennis	....	....	70	65	61	....
Nicotiana Tabacum	....	....	3	1	7	....
Sodium sulphocyanate						
Verbascum Thapsus	....	....	0	93	52	....
Rumex crispus	....	....	0	0	1	....
Daucus Carota	....	....	2	4	0	....
Oenothera biennis	....	....	63	57	53	....
Nicotiana Tabacum	....	....	9	9	14	....

SEEDS	N	0.1 N	0.01 N	0.001 N	0.0001 N	0.00001 N
Sodium iodide						
Verbascum Thapsus	....	....	37	94	62	....
Rumex crispus	....	....	0	0	1	....
Daucus Carota	....	....	4	3	0	....
Oenothera biennis	....	....	42	72	49	....
Nicotiana Tabacum	....	....	1	2	3	....
Sulphuric acid						
Verbascum Thapsus	....	....	8	35	94	97
Rumex crispus	....	....	0	1	0	0
Daucus Carota	....	....	0	12	3	7
Oenothera biennis	....	....	25	36	34	40
Nicotiana Tabacum	....	....	2	24	9	2
Potassium sulphate						
Verbascum Thapsus	....	....	87	89	100	....
Rumex crispus	....	....	1	0	1	....
Daucus Carota	....	....	1	0	1	....
Oenothera biennis	....	....	44	58	38	....
Nicotiana Tabacum	....	....	12	5	8	....
Ammonium sulphate						
Verbascum Thapsus	0	51*	92	87	98	....
Rumex crispus	0	3	7	5	9	....
Daucus Carota	0	0	1	4	15	....
Oenothera biennis	0	44*	53	54	65	....
Nicotiana Tabacum	0	36*	44	40	23	....
Sodium sulphate						
Verbascum Thapsus	....	....	91	94	88	....
Rumex crispus	....	....	2	0	2	....
Daucus Carota	....	....	1	6	0	....
Oenothera biennis	....	....	58	48	41	....
Nicotiana Tabacum	....	....	4	9	10	....
Lithium sulphate						
Verbascum Thapsus	....	....	93	91	90	....
Rumex crispus	....	....	3	0	1	....
Daucus Carota	....	....	2	3	0	....
Oenothera biennis	....	....	46	53	37	....
Nicotiana Tabacum	....	....	17	12	9	....
Nickel sulphate						
Verbascum Thapsus	....	....	63†	62	86	....
Rumex crispus	....	....	3	2	0	....
Daucus Carota	....	....	5	28	21	....
Oenothera biennis	....	....	33	40	37	....
Nicotiana Tabacum	....	....	2	13	9	....

* Little more than swelling.

† Injured.

TABLE XIV—*Continued*

Seeds	N	0.1 N	0.01 N	0.001 N	0.0001 N	0.00001 N
Zinc sulphate						
Verbascum Thapsus	....	....	41	80	97	....
Rumex crispus	....	....	0	0	0	....
Daucus Carota	....	....	2	1	1	....
Oenothera biennis	....	....	37	40	51	....
Nicotiana Tabacum	....	....	8	3	2	....
Potassium nitrate						
Verbascum Thapsus	....	....	36	82	95	....
Rumex crispus	....	....	3	2	0	....
Daucus Carota	....	....	8	18	8	....
Oenothera biennis	....	....	55	61	55	....
Nicotiana Tabacum	....	....	50	23	23	....
Ammonium nitrate						
Verbascum Thapsus	0	62	100	82	93	....
Rumex crispus	0	3	14	11	8	....
Daucus Carota	0	0	0	1	1	....
Oenothera biennis	0	70	66	68	64	....
Nicotiana Tabacum	0	54	73	34	28	....
Sodium nitrate						
Verbascum Thapsus	0	64	100	98	91	....
Rumex crispus	0	14	26	4	15	....
Daucus Carota	0	6	1	6	4	....
Oenothera biennis	0	60	67	67	50	....
Nicotiana Tabacum	0	38	34	29	11	....
Aluminum nitrate						
Verbascum Thapsus	....	....	55	98	93	....
Rumex crispus	....	....	1	1	0	....
Daucus Carota	....	....	2	3	9	....
Oenothera biennis	....	....	12	57	55	....
Nicotiana Tabacum	....	....	0	10	14	....

Seeds	N	0.1 N	0.01 N	0.001 N	0.0001 N	0.00001 N
Cobalt nitrate						
Verbascum Thapsus	....	....	31*	99	93	....
Rumex crispus	....	....	1	4	2	....
Daucus Carota	....	....	4	2	8	....
Oenothera biennis	....	....	45	57	16	....
Nicotiana Tabacum	....	....	13	15	10	....
Potassium hydroxide						
Verbascum Thapsus	....	0	84	100	98	....
Rumex crispus	....	0	6	6	9	....
Daucus Carota	....	0	7	9	4	....
Oenothera biennis	....	0	44	55	42	....
Nicotiana Tabacum	....	0	17	34	53	....
Ammonium hydroxide						
Verbascum Thapsus	....	....	1	90	95	....
Rumex crispus	....	....	0	0	1	....
Daucus Carota	....	....	0	1	3	....
Oenothera biennis	....	....	31	....	56	....
Nicotiana Tabacum	....	....	1	15	12	....
Sodium hydroxide						
Verbascum Thapsus	....	0	81	96	83	....
Rumex crispus	....	0	1	2	2	....
Daucus Carota	....	0	3	11	6	....
Oenothera biennis	....	0	50	57	0	....
Nicotiana Tabacum	....	0	21	3	16	....
Hydrochloric acid						
Verbascum Thapsus	....	....	0	38	61	92
Rumex crispus	....	....	0	0	0	0
Daucus Carota	....	....	0	5	4	2
Oenothera biennis	....	....	5	61	56	60
Nicotiana Tabacum	....	....	0	10	22	10

* Little more than swelling.

From table XIV it appears that organic acids, bases, and salts of monovalent, bivalent, and trivalent ions induce germination in darkness of seeds of *Verbascum Thapsus* (80–100 per cent), *Oenothera biennis* (40–60 per cent), and *Nicotiana Tabacum* (10–50 per cent), while they inhibit the germination of seeds of *Rumex crispus* and *Daucus Carota*. These results were confirmed in an attempt to determine the minimum effective concentration of the electrolytes. In this attempt it was found that as good germination in darkness

occurs in ten-millionth normal solutions as in one-thousandth normal solutions. These results indicate no definite relation between the nature of the ion and germination. In another series of experiments on the relation of electrolytes to germination, with seeds from another crop, it was found that the germination of *Verbascum Thapsus*, *Oenothera biennis*, and *Nicotiana Tabacum* was inhibited, while the germination of *Rumex crispus* seeds was promoted in darkness by the action of the various electrolytes. This suggests that something in the conditions of growth, maturing, harvesting, or storage may have changed the sign of the charge of the ionizable constituents of the seeds. Further work on the effects of electrolytes on the germination of these seeds is highly desirable.

Soaking in solutions of electrolytes

It is generally believed that forcing agents of germination such as light, enzymes, and electrolytes are most effective during the early stages of incubation. KINZEL (**24**) by soaking seeds of *Nigella sativa* in a solution of papayotin and asparagin for 5 hours and then in water for 24 hours secured a 30 per cent increase of germination of "light hard" seed. OTTENWÄLDER (**40**) has reported that 24 hours is not sufficient time to secure the full effect of the acid on the germination of seed of *Epilobium hirsutum*, and that about 48 hours' soaking was necessary to get the best results from the action of the acid. An attempt was made, therefore, to determine whether soaking in solutions of electrolytes could promote the germination of light-sensitive seeds.

Seeds were soaked in the various solutions for 24–28 hours and washed in distilled water until all of the solution was removed. To avoid light effects, care was taken to work in very diffuse light. The seeds were spread on filter paper in Petri dishes and placed to germinate in light and darkness respectively, at room temperature, for 8 days.

An examination of table XV *A* shows that soaking in rather strong solutions of hydrochloric acid promotes the germination in darkness of seeds of *Nicotiana Tabacum*, *Verbascum Thapsus*, *Oenothera biennis*, and *Rumex crispus*, while it hinders the germination of seeds of *Daucus Carota* in light. The beneficial effects of solutions

of sulphuric acid appear only in the germination of seeds of *Daucus Carota* in darkness. Soaking seeds of *Nicotiana Tabacum* and

TABLE XV*A*

Seeds	Light				Darkness			
	N	0.1 N	0.01 N	∞	N	0.1 N	0.01 N	∞
	Hydrochloric acid (soaked 26 hours)							
Nicotiana Tabacum	83	70	70	65	16	35	22	11
Verbascum Thapsus	34	85	87	85	1	22	24	3
Daucus Carota	0	0	0	54	0	18	25	19
Oenothera biennis	76	92	87	78	37	33	.....	8
Rumex crispus	80	84	72	.....	23	35	35	15
	Sulphuric acid (soaked 28 hours)							
Nicotiana Tabacum	.....	76	76	71	.....	10	26	21
Verbascum Thapsus	.....	79	87	81	.....	2	10	0
Daucus Carota	.....	72	66	61	.....	12	38	21
Oenothera biennis	.....	83	51	62	.....	10	11	8
Rumex crispus	.....	69	73	71	.....	24	30	31
	Sodium sulphocyanate (soaked 28 hours)							
Nicotiana Tabacum	68	.....	.....	74	48	.....	.....	19
Verbascum Thapsus	57	.....	.....	83	0	.....	.....	5
Daucus Carota	36	.....	.....	75	12	.....	.....	26
Oenothera biennis	51	.....	.....	52	0	.....	.....	12
Rumex crispus	52	.....	.....	68	54	.....	.....	24
	Sodium hydroxide (soaked 24 hours)							
Nicotiana Tabacum	0	81	61	74	0	26	25	19
Verbascum Thapsus	0	63	86	83	0	10	19	5
Daucus Carota	0	77	63	75	0	30	45	26
Oenothera biennis	1	87	42	51	0	22	12	12
Rumex crispus	0	59	76	68	0	17	26	24

TABLE XV*B*

Seeds	Percentage of hydrogen peroxide (soaked 27 hours)									
	Light					Darkness				
	50	20	10	5	∞	50	20	10	5	∞
Nicotiana Tabacum	15	75	72	56	74	6	38	81	46	19
Verbascum Thapsus	12	70	75	68	83	0	0	6	2	5
Daucus Carota	76	83	94	78	75	26	48	61	53	26
Oenothera biennis	18	33	33	40	51	0	5	12	10	12
Rumex crispus	73	66	73	77	68	43	36	70	39	24

Rumex crispus in solutions of sodium sulphocyanate appeared to promote their germination in darkness. Soaking in potassium sulphocyanate gave similar results. Soaking in solutions of hydrogen peroxide promoted the germination of seeds of *Nicotiana Tabacum*, *Daucus Carota*, and *Rumex crispus* in darkness (table XV *B*). Germination in 0.001 N sodium hydroxide was about the same as in 0.01 N. Soaking in solutions of sodium hydroxide gave increased germination in darkness of seeds of *Verbascum Thapsus*, *Daucus Carota*, and *Oenothera biennis*. These results were confirmed by another set of tests.

The reaction of the seeds to the different electrolytes indicates that the ions of the electrolytes are acting on different constituents of different seeds. While, as shown in the preceding experiment, the use of hydrochloric acid, sodium sulphocyanate, and hydrogen peroxide as substrata yields no increase of germination of *Rumex crispus* in darkness, this experiment shows that soaking for a short period (24–28 hours) in solutions of these electrolytes does promote their germination in darkness. As *Rumex crispus* seeds were brought to germination in darkness by abrading and removing the coats, and by the action of concentrated sulphuric acid, their germination may naturally be referred to coat effects, the compounds acting on some constituent of the coat. The germination of *Daucus Carota* is not so easily accounted for. The germination in darkness was only slightly promoted by increased oxygen supply and on soil as substratum. The hydrogen peroxide may yield an increased oxygen supply and thus promote the germination of these seeds, but an explanation of the beneficial effects of sulphuric acid and sodium hydroxide on the same material is not easily made unless we refer to coat effects which have not been clearly indicated by other treatment. A longer period of soaking (48 hours) might have yielded data to settle this, as well as the failure of germination of the other seeds in certain solutions.

Lipoid solvents

Finding that lipoids occur in the coats and embryos of all the seeds and in the endosperm of four of them, it was thought desirable to determine the effect of acetone, alcohol, and ether on their

germination. Seeds of each kind were soaked in acetone for 15, 30, and 60 minutes respectively, air dried for two hours, and placed under favorable conditions for germination in darkness. At the end of 8 days of incubation (in darkness) the seeds were placed in light for 8 days, where none of them germinated. Other seeds were similarly treated with alcohol with similar results. A few seeds of *Daucus Carota* and *Oenothera biennis* survived the alcohol treatment and germinated in light and darkness. Other seeds were treated with ether, as indicated in table XVI.

The results show no promotion of germination of light-sensitive seeds in darkness when treated with lipoid solvents, but rather show inhibition or diminution of subsequent germination in light. This is especially true for acetone and alcohol. Ether inhibited germination in darkness of all seeds except *Daucus Carota*, and diminished the subsequent germination in light of seeds of *Verbascum Thapsus*, *Rumex crispus*, and *Nicotiana Tabacum*. Ether treatment did not affect the subsequent germination of seeds of *Oenothera biennis* in light.

TABLE XVI

Seeds	Soaked in ether 15 minutes		Soaked in ether 30 minutes		Soaked in ether 60 minutes	
	Darkness	Light	Darkness	Light	Darkness	Light
Verbascum Thapsus	0	28	0	30	0	0
Rumex crispus	0	35	0	3	0	2
Daucus Carota	15	17	17	17	12	12
Oenothera biennis	0	76	0	74	0	62
Nicotiana Tabacum	0	43	0	64	0	31

Microchemistry

In an attempt to find the substance responding to the action of light, an examination of the seeds was undertaken by microchemical methods suggested by Eckerson (9), and the nature and distribution of the different structural and nutritive materials were determined. Much of the information thus obtained has no evident bearing on the problem of light germination and may best be presented in a separate publication. Some of the substances and conditions in these seeds which may function in light germination are fat, suberin, starch, and reaction.

Starch occurs in the endosperm of seeds of *Rumex crispus* and *Daucus Carota*. It does not occur in the embryo of any seeds under investigation. Moreover, the hydrogen ion concentration is not likely to be materially changed by such hydrolysis of starch as may occur during their germination, and therefore we need not consider starch an important factor in their germination. Since suberin is found in the coats of *Oenothera biennis* and *Daucus Carota*, but not elsewhere, it can hardly be considered a common limiting factor in the germination of the light-sensitive seeds studied. Oily or fatty substances were found in the cell contents of coats, endosperms, and embryos of each of the seeds, appearing as small droplets of substance readily stained with Soudan III or Scharlach R. These lipoids almost never occurred as continuous layers which might obstruct the entrance of water or other substance necessary for germination, but usually as emulsions of fats in the cell sap. The results of the experiments on the absorption of water support the observation that there is no important obstruction of water by the constituents of the coats. Hence suberin and lipoids need no further consideration as limiting factors in absorption of water by these seeds.

Using neutral red as an indicator, seeds soaked in water in light and in darkness, as well as dry seeds, were tested for the reaction of the different parts with results shown in table XVII.

The outstanding result of the microchemical examination is the greater acidity of seeds incubated in light as compared with those incubated in darkness. This was found to be the case in each of the five kinds of light-sensitive seeds. The embryos incubated in light had a higher hydrogen ion concentration than those of the same kind incubated in darkness. This was especially noticeable in the hypocotyls. This result is contrary to HEINRICHER'S (**21**) unsupported assumpton that the effectiveness of the fat splitting lipase was favored by the increased acid formation in darkness in *Phacelia tanacetifolia*. Moreover, HEINRICHER offered no experimental evidence of increased acid formation in darkness. Having all known external factors, except illumination, alike for the seeds under investigation, we may properly conclude that the varying factor, light, in some way brings about increased acidity of their embryos.

TABLE XVII

Seeds	Coats	Endosperm	Embryo
	Verbascum Thapsus		
Dry	Acid	Cell walls acid; contents neutral	Cell walls acid; contents neutral
Soaked in darkness	Acid	Cell walls acid; contents neutral	Outer cell walls and contents alkaline to neutral; inner cell walls acid; contents alkaline
Soaked in light	Acid	Walls acid; contents acid	Walls and contents acid
	Rumex crispus		
Dry	Acid	Outer layer acid; cell contents neutral	Walls and contents neutral
Soaked in darkness	Acid	Outer layer acid; contents mostly acid	Walls acid; contents neutral
Soaked in light	Acid	Walls acid; contents acid	Walls and contents acid
	Daucus Carota		
Dry	Outer walls acid; inner alkaline	Cell walls acid to alkaline; contents neutral to alkaline	Alkaline
Soaked in darkness	Outer acid; inner alkaline	Walls acid to alkaline; contents neutral to alkaline	Alkaline except at tip of hypocotyl
Soaked in light	Outer acid; inner alkaline	Walls acid to alkaline; contents neutral	Walls and contents acid
	Nicotiana Tabacum		
Dry	Acid	Cell walls acid; contents neutral to alkaline	Cell walls acid; contents neutral to alkaline
Soaked in darkness	Acid	Walls acid; contents alkaline to neutral	Cell walls acid; contents partly alkaline, partly neutral
Soaked in light	Acid	Walls acid; contents neutral to acid	Walls acid; contents acid except at base of cotyledons

TABLE XVII—*Continued*

SEEDS	COATS	ENDOSPERM	EMBRYO
	Oenothera biennis		
Dry	Partly acid	Slightly acid or neutral	Cell walls acid; contents neutral
Soaked in darkness	Mostly acid	Slightly acid to neutral	Cell walls acid to neutral; contents alkaline to neutral
Soaked in light	Partly acid	Neutral to acid	Walls and contents acid

Quantitative determination of acidity

To verify the results of the microchemical examination, 5 gm. of each kind of seed incubated in light for five days and 5 gm. of each kind incubated in darkness for five days were separately ground, digested in neutral alcohol and ether, and then titrated with N/10 NaOH. The results obtained were as follows:

Seed	Light	Darkness
Rumex crispus	3.5 cc.	2.8 cc.
Daucus Carota	3.3	2.8
Verbascum Thapsus	4.8	4.4
Nicotiana Tabacum	3.9	2.8

These results show greater acidity of seeds incubated in light than of those incubated in darkness, and confirm the findings of the microchemical examination. While the increase of titratable acidity was not large, it was measurable and repeatedly obtained, and apparently was sufficient in each instance to determine germination. Since light is the variable factor in this and the preceding experiment, we may properly conclude that light initiates changes which produce the increased acidity of seeds incubated in light over those incubated in darkness. These results establish the fact that light functions in some way to bring about increased acidity in these light-sensitive seeds. There remains to show in the following experiment, if possible, how the acidity is increased.

Effect of germination on substratum

Having found that the embryos of these seeds become acid in reaction by incubation in light, it was thought that testing the

reaction of the substratum after a period of incubation might throw some light on what was happening in the seeds. A small quantity of each kind of seed was soaked in distilled water, 0.01 N NH_4NO_3 solution, and 0.01 N $NaNO_3$ solution at room temperature, and the substratum tested for reaction with neutral red. The results are shown in table XVIII.

TABLE XVIII

Seeds	Soaked 18 hours in distilled water		Soaked 24 hours in 0.01 N NH_4NO_3		Soaked 24 hours in 0.01 N $NaNO_3$	
	Light	Darkness	Light	Darkness	Light	Darkness
Verbascum Thapsus	Alkaline	Alkaline	Alkaline	Alkaline	Alkaline	Alkaline
Rumex crispus	Acid	Acid	Acid	Acid	Acid	Acid
Daucus Carota	Alkaline	Alkaline	Alkaline	Alkaline	Alkaline	Alkaline
Oenothera biennis	Neutral	Neutral	Alkaline	Neutral	Alkaline	Neutral
Nicotiana Tabacum	.....	.....	Alkaline	Alkaline	Alkaline	Alkaline

From the results it appears that seeds of *Verbascum Thapsus*, *Daucus Carota*, and *Nicotiana Tabacum* excrete an alkaline substance in darkness as well as in light; that seeds of *Rumex crispus* excrete an acid substance in darkness as well as in light; and that seeds of *Oenothera biennis* excrete an alkaline substance in light.

A quantitative experiment also verifies a part of these results. Weighed quantities of each of the five kinds of seeds were incubated in light for five days in tubes containing 2 cc. of 0.01 N $NaNO_3$ respectively. The results are given in table XIX.

TABLE XIX

Seeds	Weight of seeds (gm.)	Required to titrate
Verbascum Thapsus	0.7406	1.0 cc. 0.01 N HCl
Rumex crispus	1.3385	1.5 cc. 0.01 N NaOH
Daucus Carota	0.6510	0.9 cc. 0.01 N HCl
Oenothera biennis	0.7580	0.5 cc. 0.01 N HCl
Nicotiana Tabacum	0.8403	1.8 cc. 0.01 N HCl

The longer period of incubation evidently allowed time for the excretion of a measurable amount of acid or base by each kind of seed. From these results it appears that seeds of *Rumex crispus* excrete measurable amounts of acid substance during incubation, while the other kinds excrete alkaline substances.

Enzymes

The favorable effects of light on the germination of seeds of *Veronica peregrina* in the early work of HEINRICHER (**19**) was referred to its effect upon chemical actions connected with the reactivation of reserve materials, and later (**21**) to its effect upon enzyme activity in the production and digestion of stored foods. He (**22**) referred the retarding effect of light on the germination of seeds of *Phacelia tanacetifolia* to its photochemical action on reserve materials, and assumed that the effectiveness of the fat splitting lipase was favored by the increased acid formation in darkness, while the irrefrangible light or the rays of the first half of the spectrum interfered, neutralizing the acid and thereby checking the decomposition of fat.

It seemed possible that enzymes of some kind might be active agents, and light the stimulus or trigger in the germination of certain seeds. Just what kinds of enzymes function most in the germination of light-sensitive seeds has not been shown. To determine whether proteolytic enzymes were the important enzymes for the seeds, as LEHMANN and OTTENWÄLDER (**36**) believed for seed of *Epilobium hirsutum*, seeds of *Verbascum Thapsus* and *Nicotiana Tabacum* were incubated in light and darkness respectively for four days and promptly ground in a little 50 per cent water solution of glycerine to which a crystal of thymol had been added. Small drops of extract from each kind of seed were put on nutrient gelatin according to the method of GIESEN (**16**). After 30 minutes the extract was taken up with soft filter paper. There were very shallow pits formed where the extracts incubated in light had been. There were also shallow pits formed on the gelatin where the extract incubated in darkness had been. In fact, the pits produced by the extract germinated in darkness were deeper than those produced by the extract incubated in light. To verify these observations, the tests were repeated after allowing a more complete extraction of the enzyme. The extracts of seeds incubated in light were put in light, and the extracts of seeds incubated in darkness were put in darkness. The following day the same tests were repeated. Extracts from each lot of seeds were tested for their action by putting loopfuls on gelatin. After 30 minutes the extracts were removed separately, when it was

found that well defined pits had been formed in the gelatin. Moreover, where the extract was left on the gelatin for 24 hours, the pits became quite deep, even though there was abundance of thymol to inhibit bacterial action. These results were confirmed by the method of GRÜSS (**17**).

Since the activity on gelatin of enzymes of seeds incubated in darkness was equal to or greater than that of seeds incubated in light, the favorable effect of light on germination of *Nicotiana Tabacum* and *Verbascum Thapsus* cannot be referred to activation of proteolytic enzymes.

It has already been seen that starch does not occur in the embryos of any of these light-sensitive seeds, and that it occurs only in the endosperms of *Daucus Carota* and *Rumex crispus*. From these facts it is evident that hydrolysis of contained starch can increase the hydrogen ion of the embryos little if any. It has been seen that proteolytic enzymes develop equally well in darkness and light in these seeds, hence they can be rejected as important factors in determining light germination. Also, incubation in light does result in increased acidity of embryos over those incubated in darkness.

It has been shown that the embryos of these seeds all contain fatty substances. The generally accepted method of demonstrating the presence of lipolytic enzymes is by the increase of acidity in the presence of fats. Inasmuch as development of acidity in the presence of light and fatty substance has been clearly demonstrated, it may be concluded that light activates the lipolytic enzyme to split the fatty substance to yield an acid. The results obtained with enzymes of seeds of *Verbascum Thapsus* and *Nicotiana Tabacum* do not support HEINRICHER'S (**22**) assumption that light inhibited the action of lipase in seeds of *Phacelia tanacetifolia*. On the other hand, the results indicate that light favored the action of lipase in seeds of *Verbascum Thapsus* and *Nicotiana Tabacum*.

Discussion

COAT EFFECTS

The light relation of seeds of *Rumex crispus* is largely one affecting the coats, as is indicated by increased germination in darkness following abrasion and removal of coats, treatment with

concentrated sulphuric acid, and increased oxygen pressure. Light may bring about some change in the coats of *Rumex crispus* to admit oxygen or other required substance, or permit the escape of some inhibiting substance such as an organic acid. It may change the relation of the lipoids from the oil water phase to the water oil phase, or break up a nearly continuous oil layer in the coat, thus allowing entrance or escape of some limiting factor. The presence of lipoids in the coats and the excretion of an acid instead of an alkaline substance during germination suggest that an enzyme acting in the coats hydrolyzes the lipoids, thus yielding acid and making the coats permeable to some required substance, or permitting the elimination of some inhibitory substance.

There is some evidence of a coat effect in the germination of seeds of *Oenothera biennis*. While abrasion of the coats does not yield increased germination, hot water treatment and sulphuric acid treatment both yield considerable increases of germination in darkness. The presence of lipoids in the coats suggests the same explanation of the action of light as in the seeds of *Rumex crispus*, with the addition that the light may also have a beneficial effect on the constituents of the embryo.

In the seeds of *Nicotiana Tabacum*, *Verbascum Thapsus*, and *Daucus Carota* there is little evidence of coat effects, there being no increased germination caused by abrasion, sulphuric acid treatment, hot water treatment, or increased oxygen pressure. The only results suggesting coat effects are increased germination of *Daucus Carota* and *Nicotiana Tabacum* when soaked in hydrogen peroxide. This increased germination might be referred to the effects on the embryos.

The seeds of this investigation fall into three groups. The first is represented by the seeds of *Rumex crispus*, in which the coats must be made permeable to some external or internal substance by light, abrasion, or other agency before abundant germination occurs. The second group is represented by the seeds of *Oenothera biennis*, whose germination is partly dependent on the coats being made permeable, and partly on the activation of the embryos by light or chemical agencies. The third group is represented by seeds of *Nicotiana Tabacum*, *Daucus Carota*, and *Verbascum Thapsus*,

whose germination is not increased simply by making the coats permeable, but requires the action of light or a suitable substitute to induce good germination.

Microchemistry

The results of the various mechanical, physical, and chemical treatments of the light-sensitive seeds have offered few suggestions as to the nature of the effects of light on their constituents in inducing germination. The substitution of these various agencies for light has contributed little to an acceptable explanation of how light functions to bring about germination. These treatments, however, have served to localize the action of light and to determine the part of the seed affected. On the other hand, the microchemical examination yielded results which point to an acceptable explanation of the action of light on light-sensitive seeds. The outstanding findings of the microchemical studies were abundance of lipoids in each kind of seed and increased acidity of seeds incubated in light. Thus there are linked together light, lipoids, and increased acidity.

Enzymes

Since starch and other carbohydrates were not found in the embryos of these seeds and in the endosperms of but two of them, it is not necessary to give serious consideration to the probable reaction of the products of their hydrolysis. Moreover, since proteolytic enzymes were found to be equally active in light and darkness in *Nicotiana Tabacum* and *Verbascum Thapsus* seeds, they need not be considered as important causes of increased acidity of the seeds incubated in light. It remains to be considered whether the products of the hydrolysis of the lipoids are the cause of the increased acidity in light.

The development of acidity in the watery extract of an oily seed like that of the castor bean is generally considered evidence of the presence of lipase. Such development of increased acidity in light was demonstrated quantitatively for four of the five kinds of seeds, thus confirming the results of the microchemical examination, and giving reasonable ground for inferring that lipase splits the fats thus yielding fatty acids in seeds germinated in light.

Again, the presence of neutral or very faintly alkaline fats in the cells of the dry embryos and the development of acids in embryos incubated in light and no change or development of slight alkalinity when incubated in darkness is very significant. It is generally assumed that increased acidity of fatty substances indicates hydrolysis due to the action of enzymes. If this assumption be granted, the admission is necessary that light initiates processes which in some way result in increased acidity, which is followed by germination, and that where light is not admitted acidity does not develop sufficiently to cause good germination. Three explanations of how light acts may be offered: (1) light may act directly to split the fats to fatty acids and glycerine; (2) light may activate the lipolytic enzyme which splits the fats; (3) light may initiate some change that produces a little acid which may activate the lipolytic enzyme which splits the fats.

While it is possible and even probable that light can act directly on the inclusions of cells to produce such changes as the formation of acid, it is hardly necessary to make this assumption. The proteolytic enzymes become active in the absence of light when the seeds are put under the usual conditions for germination. A certain percentage germinate in darkness even though they have not been treated with electrolytes or other stimulating agencies. Moreover, the amount of acid produced, though small, is relatively more than might be expected from the chemical action of light on lipoids. The evidence of the existence of lipase rather indicates either of the other explanations as much more acceptable. There is little choice between light activating the enzyme and light initiating some change which produces a little acid which may activate the lipolytic enzyme which splits fats. In either case light is the stimulus which initiates the changes leading to germination.

Summary

1. The seeds of *Rumex crispus*, *Datura Stramonium*, and *Phoradendron flavescens* were found to be light sensitive. The germination of seeds of *Rumex crispus* and *Phoradendron flavescens* was promoted by light; the germination of seeds of *Datura Stramonium* was hindered by light.

2. Abrasion and removal of coats (ovary walls) of *Rumex crispus* seeds promoted their germination in darkness.

3. Treatment of seeds of *Rumex crispus* and *Oenothera biennis* with concentrated sulphuric acid caused an increase in the percentage of germination in darkness.

4. No reciprocal relation between the effects of light and temperature was found.

5. Light was not necessary for the absorption of sufficient water for germination.

6. Injection of water did not yield increased germination in darkness.

7. Almost all kinds of single electrolytes, regardless of the nature of the ions, seemed to promote germination of seeds of *Oenothera biennis*, *Nicotiana Tabacum*, and *Verbascum Thapsus* in darkness.

8. Embryos of seeds incubated in light became more acid than those incubated in darkness.

9. Light seemed to activate lipolytic enzymes which hydrolyzed fats to fatty acids.

10. The germination of seeds of *Rumex crispus* in darkness was promoted (increased) by hot water treatment, abrasion, treatment with concentrated sulphuric acid, increased oxygen pressure, fluctuating temperatures, and soaking in solutions of hydrochloric acid, sodium sulphocyanate, and hydrogen peroxide.

11. The germination of seeds of *Nicotiana Tabacum* in darkness was promoted by soaking in solutions of hydrochloric acid, sodium sulphocyanate, and hydrogen peroxide, as well as by the use of many single electrolytes as substrata.

12. The germination of seeds of *Verbascum Thapsus* in darkness was promoted by the action of light, fluctuation of temperature during incubation, alternating high and low temperatures, soil, and many single electrolytes as substrata.

13. The germination of seeds of *Oenothera biennis* in darkness was promoted during certain seasons by hot water treatment, sulphuric acid, preliminary incubation at low temperature, incubation in alternating high and low temperatures, and single electrolytes as substrata.

14. The germination of seeds of *Daucus Carota* in darkness was promoted by increased oxygen pressure and preliminary incubation at low temperature, while it was hindered by soaking in hydrochloric acid and by the use of single electrolytes as substrata.

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ECOLOGY OF TILIA AMERICANA

II. COMPARATIVE STUDIES OF THE FOLIAR TRANSPIRING POWER

JAMES E. CRIBBS

(WITH TEN FIGURES)

A comparative study of the foliar transpiring power of *Tilia* as recorded in the field for dune environments (1) preceded this work, which is an extension of the former investigations, and is concerned with the data recorded for the same species as obtained from a wide range of habitats on clay soils.

The methods employed were essentially the same as described in the former discussion of the dune series. A 3 per cent cobalt chloride standard paper was used in all the work for determining the relative transpiring power, and was applied by means of the clip devised by LIVINGSTON (4). As in the former experiments, readings were taken on two leaves at each station, the same leaves being employed in subsequent readings. Records were taken at approximately hourly intervals, and as recorded represent the average of four to six readings. Curves are plotted for both leaves. The slight difference observed in the readings for the two leaves, which occasionally became considerable, was in most instances attributed to the relative maturity and specialization of the epidermis and cuticle.

Measurements of the chief environmental factors were recorded, and special features of the environment taken into consideration. The chief factors measured were evaporation, relative humidity, atmospheric temperature, soil temperature, wilting coefficient, and growth water. The occurrence of alternate sun and shade, velocity of the wind, fog, and passing thunder showers were special features which were found to bear a definite relation to the oscillating behavior of the transpiration stream. Measurement and computation of these factors were carried out in the same manner as in the preceding experiments.

Nine different stations were chosen, representing the range of habitats frequented by *Tilia* on clay soils. Stations *F*, *G*, and *K* are located on the old Lake Chicago plain, *K* being in Washington Park at Chicago, while *F* and *G* are located in an open forest on the flood plain of the Des Plaines River. These are environments having a strong prairie influence both as to environmental factors and flora composition. Station *H* is located in a mesophytic forest on a glacial upland in western Pennsylvania, where the chief components of the lower flora include such members as *Adiantum, Actaea alba, Osmorrhiza, Botrychium virginianum, Aralia quinquefolia*, etc. Station *I* is near *H*, but occupies a position at the edge of an evergreen swamp which lies between glacial moraines. The soil here is of heavy blue clay overlaid by a few inches of rich humus. The undergrowth is composed largely of *Taxus, Arisaema, Veratrum viride*, and *Symplocarpus*. Station *J* is located at the foot of a steep east-facing embankment at the edge of a creek where the water content of the soil is always high and insulation is low. Station *M* is in a partially wooded rocky ravine where the chief members of the ground flora are *Adiantun, Osmunda, Arisaema*, etc. Station *N* is near the opening of the same ravine in a more exposed location on alluvial soil washed down from above by the stream. Station *L* is on the flood plain of the Neosho River in Kansas, and represents the species on the western prairie tension line.

This series includes *Tilia* both in its normal environment, the mesophytic forest, and in abnormal ones when considered from an ecological standpoint. It also includes the species near the center of its distribution and on the limits of its range, where it is eliminated by members of another climax series, the prairie. Data have been presented in graph form to better illustrate such correlations as exist between the recorded factors. Graphs for all readings are not presented, because of the recurrence of very similar data at some of the stations. Those recorded, however, represent all the essential facts observed in the work at the various stations.

Normal features of transpiration curve

It has been a commonly observed feature in work on foliar transpiration that the curve representing its index rises quite

rapidly in the morning, beginning at dawn or shortly after. This early rise was attributed by LLOYD (7) to the opening of the

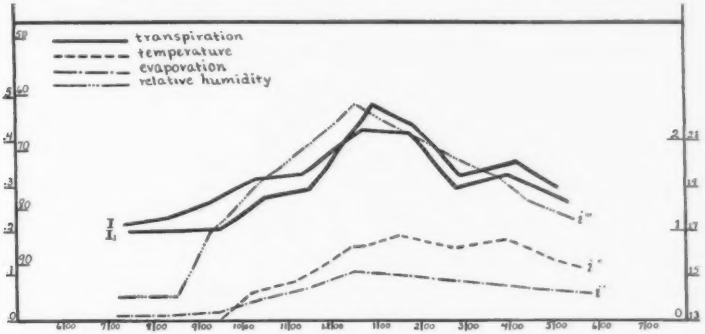

FIG. 1.—Data taken at station *I* on June 7, showing approximate concurrence of maxima in different curves; legend applies to all figures except fig. 7.

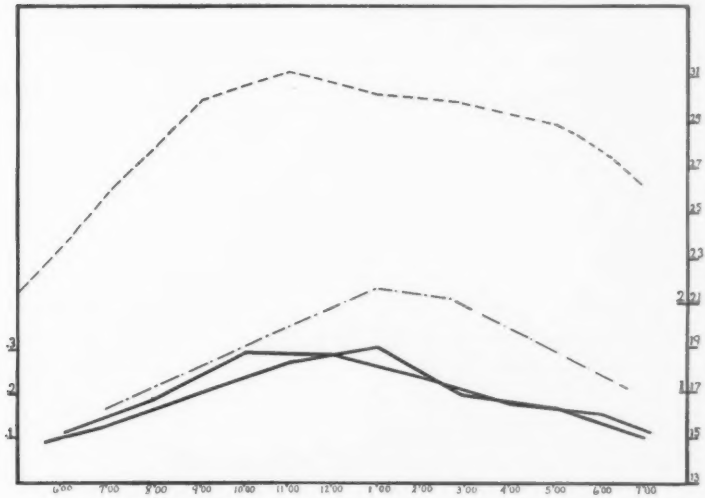

FIG. 2.—Record of data for station *K*, taken in Washington Park, Chicago, August 16; note gradual rise and decline of transpiration curve.

stomata under the influence of light. That there is a sudden opening at this time has been verified by direct examination recently by SAYRE (8). In working on *Nicotiana* and *Verbascum*

he found that the stomata opened rapidly, beginning at about 5:00 A.M. and reaching a maximum about 8:00–9:00 A.M. The study

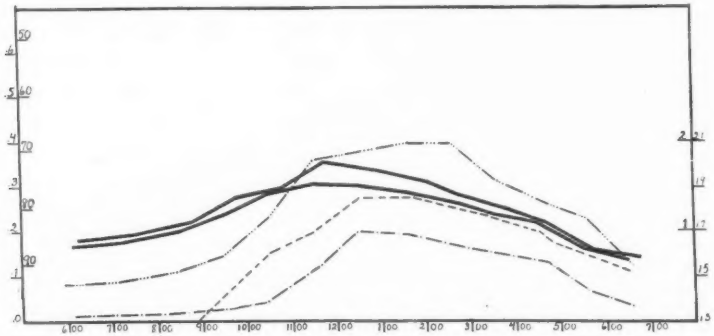

FIG. 3.—Records for station *N*, taken September 2, showing gradual rise and decline in transpiration index, with approximate concurrence of maxima.

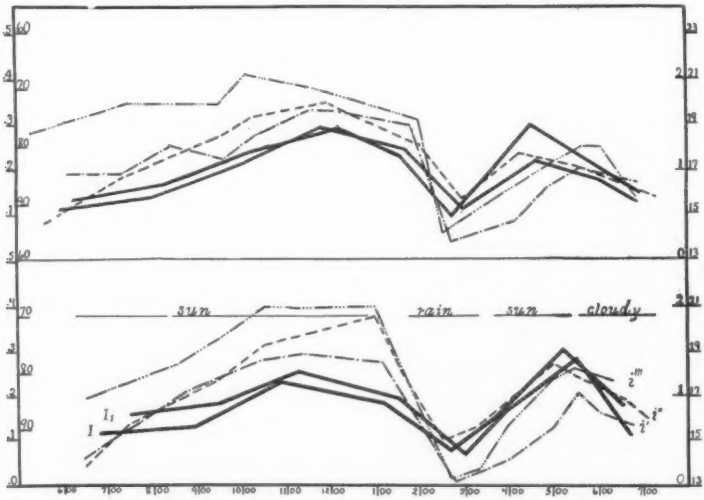

FIG. 4.—Graphs for stations *H* and *I*, taken on June 8, illustrating pronounced depression in transpiration index caused by precipitation; note that both temperature and evaporation curves show like depression and subsequent rise.

of *Tilia* in its more normal habitats on clay has shown a variation from this behavior. Figs. 1, 2, 3, and 4 show that, quite unlike the customary behavior in positions strongly exposed to light, the

transpiration index as recorded in forest habitats more frequently showed a slow steady rise, beginning with the morning opening of the stomata and continuing to a maximum which usually occurred about midday. The maximum was approximately three hours later in the forest than on the open dune sands. It was also much lower relatively than was found to be true for the sand environment. In only one instance was the coefficient observed to reach 0:5 on the forested clay, while in the former case it not infrequently

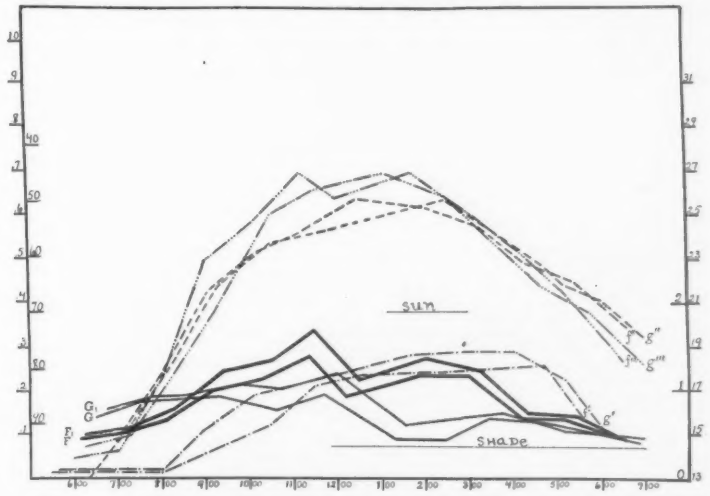

FIG. 5.—Data for stations *F* and *G* in prairie flood plain forest near Chicago; both readings for August 18; stronger saturation deficit recorded for station *G* than for *F*.

attained 0:9. Following the morning maximum, a feature of the transpiration curve, as pointed out by various investigators, is the depression which occurs, causing a divergence from the curves representing temperature, relative humidity, and evaporation. This has been thought to be due to the creation of a deficit of water in the mesophyll cells. Such depressions are strongly evident in the dune graphs, but were inconspicuous throughout the work on *Tilia* in clay habitats. Fig. 5 shows a deficit depression in the graph representing station *G*. It is less evident at station *F* for the same day. Figs. 2 and 3 show a slight divergence from the

evaporation curve, but in all instances the deficit is relatively slight when compared with that recorded in the former studies of this species. The fall of the transpiration curve in the afternoon was just as gradual and slow as the morning rise, by 7:00 P.M. or soon after, reaching approximately the same level as that recorded for 5:00 or 6:00 A.M. preceding the first rise.

The prominent features of the curves as found in this series of studies were a gradual rise, a low maximum which comes approximately at noon, the absence of a conspicuous saturation deficit, and the gradual decline to the night rate of transpiration. In the records obtained on the dunes there was very generally a depression about midday, and the curve was frequently characterized by a secondary rise developing a lower mode in the middle of the afternoon. This was followed by the evening decline. Such development of a secondary mode in the transpiration curves was not a feature of the records obtained on clay soils, but was observed in a few readings only, when it was attributed to the influence of special factors such as the rapid decrease in relative humidity following a period of precipitation in the early afternoon (fig. 4).

Effect of environmental factors upon transpiration

The foliar transpiration stream undergoes various fluctuations, occasioned by the stimulus of certain factors which by temporarily exerting a dominating influence may bring about a pronounced and rapid response in the rate of water loss.

PRECIPITATION.—Passing thunder showers usually caused the coefficient of transpiration to fall very rapidly. Fig. 4 shows the effect of a shower at stations *H* and *I*, these graphs being plotted from data secured on June 8. The general atmospheric conditions other than recorded in the graphs are indicated in the lower figure. It will be seen that at the two stations the same depression appears during the period of precipitation. The corresponding depression in evaporation, temperature, and relative humidity curves shows these factors all working together to produce the same result, namely, a lower transpiration rate. Immediately following the shower, which lasted one and one-half hours, there was a sudden and rapid rise in the transpiration curve, accompanied by a cor-

responding elevation on those of temperature, evaporation, and saturation deficit of the air. The height of the rise was on the whole rather unexpected, inasmuch as the late afternoon was regularly characterized by a steady decline, during which time the stomata were closing. Similar reactions during brief periods of precipitation were recorded during investigation on the dunes, where the depressions were commonly less pronounced.

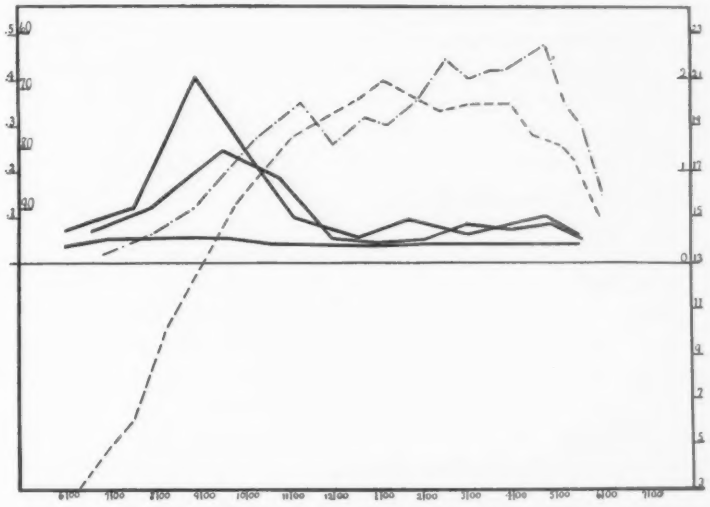

FIG. 6.—Data for station *J*, taken September 3, showing depression in transpiration as result of visible wilting caused by abscission; third solid line represents cuticular transpiration as recorded for adaxial side of leaf; note low temperature in morning.

ABSCISSION.—Fig. 6 shows a curve which is strikingly different from the typical one recorded during this work. It is characterized by a rapid rise to a fairly high maximum which occurred early, about 9:00 A.M. Following the maximum there was a decline, which by midday had almost reached the level of cuticular transpiration. This condition prevailed throughout the remainder of the day, there being a slight and very gradual rise until about 5:00 o'clock. The mesophyll saturation deficit recorded is very conspicuous. This curve is very similar to those described as occurring at stations *A* and *B* on the dunes taken on August 26 (fig. 9, graph 3). In that

instance it was found that the low curve was caused by the soil water being reduced to the wilting coefficient. Such could not be true in this case, however, as the growth water was in excess all the time. The cause of depression at station *J* was found to be associated with abscission. This was likewise an influencing factor in the similar depression formerly referred to, being induced there by the inadequacy of water supply.

WILTING COEFFICIENT.—The effect produced on transpiration when the soil water falls to the point of the wilting coefficient was not observed in any of the work on clay soils, for the growth water content at the time of all readings was found to be adequate to meet the requirements of the plant. Its effect has been referred to, however, in connection with the dune data, where in the dune forest it develops in August. Transpiration under such conditions remains almost entirely cuticular, with the exception of a slight rise in the early morning, when the reserve water accumulated during the night is being utilized.

RELATIVE HUMIDITY.—Relative humidity is considered one of the most potent of the atmospheric factors influencing the transpiration stream. It is the direct cause of the establishment of a diffusion gradient between the internal atmosphere of the leaf and the external atmosphere. Other physical factors initiate change in relative humidity, such as temperature, but because transpiration is a molecular diffusion problem, it should be interpreted as bearing its closest relation to those factors which initiate and directly influence this process. Relative humidity has this close relationship to the foliar water loss, and slight sudden changes in this factor are usually registered in the transpiration curve, even though the porous cup makes no record of it. Reference to fig. 9, graph 2, will illustrate this relation. CURTIS (**2**), in observing the effect of relative humidity, states that an increase of 8 per cent was followed by a pronounced reduction in the transpiration rate.

EVAPORATION.—The relative humidity and evaporation curves do not always show so close a parallel as might be expected (fig. 9, graph 3), so that in some instances there is greater correlation between those representing temperature and evaporation than between relative humidity and the latter. This divergence is very

largely due to the effect of winds, which, without affecting the humidity, accelerate the loss of water from the porous cup, and may to a less degree affect the transpiration rate. The atmometer shows greater sensitiveness to the influence of wind than does the leaf.

TEMPERATURE.—Temperature exerts a very important influence in the transpiration process by affecting the surface tension films of the mesophyll cells and changing their rate of molecular diffusion. LIVINGSTON (**6**) has referred to temperature as the probable controlling factor in causing fluctuations in the transpiration stream. An increase in temperature accelerates the diffusion from the mesophyll cells, setting up an increase in the vapor pressure within the leaf. At the same time it also increases the saturation deficit of the external atmosphere, and sets up between the internal and external atmospheres a steeper diffusion gradient, thus leading to a more rapid diffusion of water vapor through the stomata.

Temperature, evaporation, and relative humidity do not explain in full the variation recorded in the foliar transpiring ability of the plant from day to day. Figs. 2 and 5 show transpiration curves typically alike except for a slight depression in the latter at noon. The averages of the relative foliar transpiring power in each of these two cases are almost identical, being 0.198 and 0.193 respectively, yet the atmospheric factors were all exerting the greater physical demand for water at station *K*. Again, if we compare figs. 2 and 3, we find two transpiration curves of the same type, that in fig. 3 being throughout the day approximately 0.05 higher than that at station *K*. Despite this discrepancy the physical factors would call for a transpiration rate considerably lower at station *N* than at station *K*. Moreover, if we compare the graphs represented in figs. 1 and 3, we find that fig. 1 has a higher transpiration rate throughout the afternoon, although the relative humidity is almost the same, and both evaporation and temperature are lower, thus theoretically calling for a lower rate. This failure of the transpiration stream to bear a consistent relationship to the factors of temperature, evaporation, and relative humidity was formerly interpreted as being the influence of stomatal movements, but the fallacy of such interpretation has been pointed out by LLOYD (**7**) and others. Direct investigation has shown that the stomata open quite early

in the morning, reaching a maximum early (8:00–10:00 A.M.), after which there is a gradual closing until dark, about which time they approximate the closed night condition. During the day it seems that the maximum water loss is always less than the maximum amount which may be diffused from the open stomata, so that the lower general average for certain days must be referred to other causes.

On the sand dunes there is a strong tendency to high transpiration, as is evidenced by the graph representing station *D* for September 2 (**1**, fig. 8). The evaporation and relative humidity in this instance were closely similar to that recorded for station *N* (fig. 3). The temperature, which registered the greatest degree of difference, averaged about 4 per cent higher, yet the transpiration index was just 100 per cent greater, averaging 0.23 in the latter instance and 0.46 in the former. Thus in any given situation the transpiration may be high or low irrespective of the relative humidity, temperature, and evaporation, although these factors are certainly instrumental in influencing fluctuations in the transpiration stream. In other words, *Tilia* on the open dunes will transpire more actively than the same species in the mesophytic forest, irrespective of atmospheric conditions; and, with similar weather conditions prevailing, in clay environments there may be a considerable variation in the transpiration index from day to day. It is the opinion of the writer that the former of these conditions may be associated with structural differences, and investigations are being made with the hope of giving further light upon this phase of the problem.

GROWTH WATER.—The relation of growth water to the transpiration index has proved interesting. This is the soil moisture content minus the wilting coefficient as expressed by FULLER (**3**). Fig. 7 illustrates the relation between growth water and transpiration as recorded in the field during the course of investigation. The five stations located on the dune sands are represented by *A*, *B*, *C*, *D*, and *E*. It will be noted that the growth water is very low, ranging from an average of 1.25 to 2.60 per cent. Furthermore, the water loss by transpiration is found to be greatest at the most exposed station, where the growth water average is lowest, and decreases rapidly to a level, which is found at stations *A* and *B*

to be similar to the average rate for the clay positions, where the growth water percentage is relatively high. The average transpiration rate for the mesophytic clays is approximately one-half that exhibited on the open sands. The growth water in the mesophytic forest, despite the lower transpiration rate there, is on the average at least six times as great as on the dunes.

Reference to data for stations located on clay shows that the growth water for these positions fluctuates about 18 per cent,

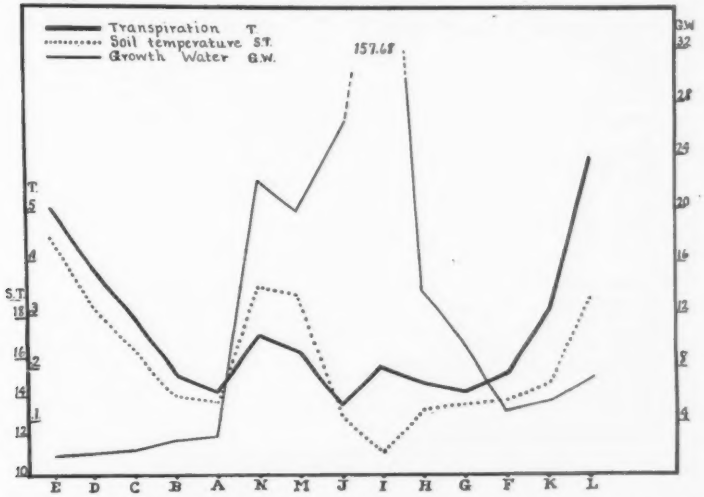

FIG. 7.—Data for soil temperatures, growth water, and transpiration as recorded at all stations on sand and clay; note high transpiration associated with low growth water and high soil temperatures.

being above more often than below this average. Notwithstanding the fact that growth water is always relatively abundant, the transpiring ability is proportionately low, with but two exceptions not exceeding 0.5 at any time during the investigations. The close approximation of the average transpiration rate on the mesophytic clay soils to that of stations *A* and *B* in the dune forest is also evident in fig. 7. Thus the comparative equality in the transpiring power, while the growth water ranges from an average of 2.25 per cent at station *A* to 157.68 per cent at station *I*, strongly indicates

that growth water influences the transpiring ability of the foliage leaves to a less extent than do the atmospheric factors. The only critical evidence of growth water influence during these studies was when it diminished until it approached the wilting coefficient. Visible wilting may then occur, accompanied by a rapid reduction in transpiration until it becomes almost entirely cuticular. Repeated reduction to the wilting coefficient was found to induce early abscission of the leaves, a phenomenon found to take place earlier in the dune forest than upon the open sands of the same region. The effect of abscission upon the foliar transpiring ability has already been shown to be similar to that occasioned by the development of a wilting coefficient in the soil. Thus while it is essential that growth water be available for the plant, there was little evidence that it exerts a conspicuous influence in the daily variation and hourly fluctuation of the transpiration stream, for differences in average available water ranging from 2.5 to 157 per cent show no corresponding variations in transpiring power.

SOIL TEMPERATURE.—It was not determined in the field to what extent soil temperatures influenced the transpiration stream. A few very significant features are evident from the data, however, as when the average foliar transpiring power for each of the stations is considered, and correlated with the average soil temperatures for the same stations, taken on the same days. This comparison is indicated in fig. 7 by the heavy solid and dotted curves, the latter being the curve for soil temperature. It will be noted that the temperature of the soil is high where the transpiration is high and low where the transpiration is low. There was but one instance when a decrease in soil temperature was not accompanied by a corresponding reduction in the transpiration index, this being registered for the swamp habitat. A close parallel was found between average soil temperatures and average transpiration indices.

A second feature is recorded in the relations of growth water and soil temperature. It will be noted that the soil temperature decreases as the growth water increases, so that the lowest soil temperatures are found where the water is most abundant and the highest temperatures where the water is least. The records for

stations *M* and *N* (fig. 7) show a variation from the behavior recorded for the other stations. The readings for these two were taken on one day only, and hence, not being an average of several days' data, are not considered typical. This is especially true as these records were taken in early September during a period of dry hot weather, and hence represent maximum figures for these stations. There is no doubt that the average transpiration and soil temperatures would have been very close to those of station *J* had readings been taken in the late spring and early summer, as was done at the other stations. To what extent this low soil temperature is associated with low transpiring power and high soil temperatures with high transpiring power, cannot be adequately stated at present, but it is known that low soil temperatures produce an inhibiting effect on water absorption by the root system, and would therefore be expected to lead to a lower rate of water loss from the leaf.

The average soil temperature of station *E* is slightly more than double that recorded for station *I*, and the fact that the transpiration index is likewise a little more than doubled is very suggestive. The close parallel recorded between average soil temperatures and average transpiration indices throughout these experiments may be considered evidence that this factor is influential in limiting the foliar water loss.

SUNLIGHT.—Sunlight directly or indirectly produces an effect upon transpiration, inducing a rise in its index. This was pointed out by LIVINGSTON (5) as the result of studies on the effect of light intensities upon the transpiration rate in *Xanthium*, *Physalis*, and *Martynia*. Fig. 6 shows in the morning rise a response to sunlight. The transpiration index in this instance did not show the characteristic response until two hours after daylight, whereas usually the rise begins about dawn. On this day transpiration increased rapidly, beginning when the sunlight fell directly upon the station. The failure to develop an earlier response is attributed to the very low temperature, which was at that time but slightly above the freezing-point. Sunlight falling upon the leaf is followed by the absorption of certain rays which leads to an increase in temperature sufficient to accelerate the diffusion of water from the mesophyll

cells, thus affecting the diffusion gradient and resulting in a greater water loss.

Comparison of swamp and upland mesophytic types

As previously stated, station *H* is located in a typical upland mesophytic forest on mixed morainic clay, and station *I* is located on the border of a swamp where the undergrowth is composed largely of *Taxus* and spring perennials, and where the tree stand

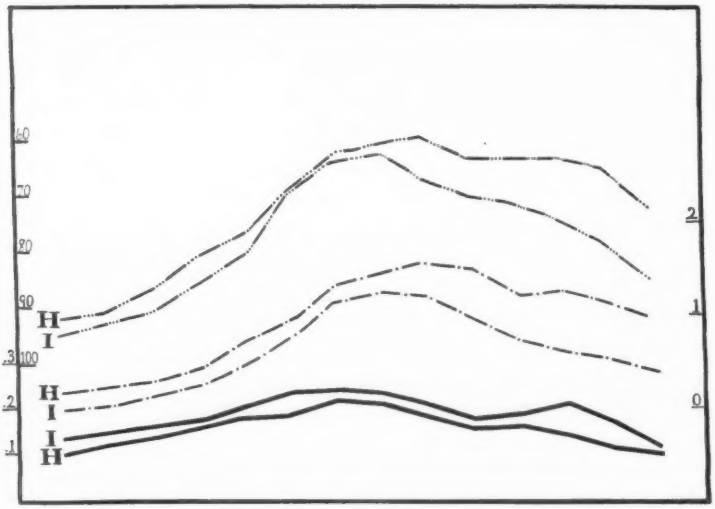

FIG. 8.—Relative humidity, evaporation, and transpiration for stations *H* and *I*, showing average of 5 days' readings at each station.

includes *Tsuga*, *Fraxinus*, and *Acer*. Beneath the humus at station *I* is a heavy blue clay soil which is saturated during practically the entire growing season, and *Tilia*, as do most other forms of vegetation in similar situations, grows to form a low broad hummock, because the roots, being unable to penetrate deeply, spread out on the surface. In this supersaturated environment a peculiar behavior was observed in the transpiration stream. This is shown in fig. 8, which is a composite graph, each curve representing the average of five separate days' readings and including relative humidity, evaporation, and transpiration. It will be noticed that both

relative humidity and evaporation show curves which indicate greater mesophytism at station *I* than at station *H*, but contrary to expectation the transpiration record at the latter is higher throughout the period than in the mesophytic forest. The transpiration curve was higher than that recorded for the much more open forest on the old Lake Chicago bed, where there is a strong prairie influence. Fig. 7 shows that, although the transpiration is relatively high, as on the sand series, the factors of soil temperature and growth water at station *I* are excessive in their extreme opposite relation to the dune condition. Insolation is probably the most influential factor leading to a higher transpiration at this place. It would seem from the relations worked out between transpiration and stomatal aperture by various investigators that the stomata should not prove a limiting factor at the forest station, for the light intensity would seem adequate to insure an opening there which is sufficient to permit a much greater diffusion from the leaves than actually occurs. That increased exposure to light is accompanied by the absorption of light rays by the mesophyll which produce heat and a greater molecular pressure on the water films in the cell walls, and hence leads to a more rapid diffusion of water, seems a reasonable explanation and one which is substantiated by the work of LIVINGSTON (5) on the effect of this factor on transpiration.

Daily variation in transpiring ability

In the former discussion of transpiration on the dunes it was pointed out that if the index of foliar transpiring power were to be utilized in an endeavor to measure the mesophytism of a plant, it should be based on the records of more than a single day, since the variability in the foliar transpiring power is very noticeable from day to day. There is a great daily fluctuation in the transpiring power, just as there is a great hourly fluctuation, and both hourly and diurnal variations are more pronounced on the dunes and prairie than on the forested clays.

Fig. 9 indicates the transpiring ability as recorded at station *C* on the dunes for July 16, 21, and August 26, and it will be observed that on these three days there chanced to be striking differences in the course of the curves representing water loss from the leaves.

The curve for July 16 shows that it is characterized by a late morning rise, a feature quite unusual for the dune series. In addition, the maximum is reached at 1:00 P.M., when the usual occurrence in this environment was a depression at that hour. There was also a high transpiration recorded during the afternoon without the appearance of a secondary mode at 4:00 to 5:00 P.M.

The first of these features, the late morning rise, is attributed to the atmospheric conditions, which show a very low temperature

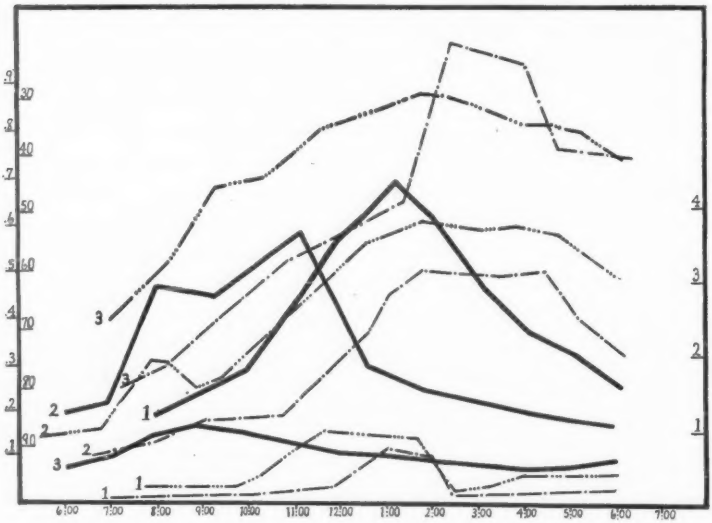

FIG. 9.—Record of readings at station *C* for July 16, 21, and August 26, showing 3 distinct types of curves although records were taken from same leaves.

(about 17°), but especially a low evaporation rate and a high relative humidity. The general weather conditions show a cloudy period, following precipitation from about 5:00 to 6:20 A.M. At 10:00 A.M. the weather became clear, followed by a slight increase in temperature, evaporation, and saturation deficit of the air. Notwithstanding the slow increase in these factors, the foliar transpiration was found to increase much more rapidly in proportion. Thus the maximum transpiration index was greater than was observed to occur under similar conditions on the clays, except

on the prairie, where the factors in general approximate those of the open sands of Lake Michigan, except for the soil type. The high maximum is attributed to the late morning rise and the failure to develop a saturation deficit in the leaves; the factors tending to this end all being impotent throughout the day, namely, high temperature, high evaporation, low relative humidity, high wind velocity, and wide open stomata. A light precipitation in the early afternoon was accompanied by a lowering of temperature and evaporation and an increase in relative humidity to a point approaching saturation, while the transpiration index fell more slowly than was commonly true under such circumstances.

Transpiration curve no. 2 represents the relative foliar water loss for July 21. This curve is characterized by a very early rise because the weather was at that time clear. The rapid ascent was interrupted at 8:00 A.M. owing to the influence of relative humidity. At this time there was a period of cloudiness for an hour or more, when a thunder shower passed just southward without giving precipitation at the station. At 11:00 A.M. the transpiration index had attained its maximum, and conspicuous depreciation between the curves of water loss and evaporation was then developed. There occurred then a period of six hours when the factors for high transpiration increased, but the index nevertheless continued to fall throughout the period. No visible wilting took place on this day, and there appears no evident reason why the transpiration index should not have exceeded that for July 16, judging from the relative humidity, evaporation, and temperature. The difference might be attributed to the less amount of growth water (4.537 per cent) in comparison with that of the latter date (5.910 per cent). I do not believe, however, that the quantity of available water influenced the transpiration very strongly in this instance, for, as already stated, higher indices were regularly attained on the open sands where the growth water was as low as 1.25 per cent. It would seem that the depression takes place at the time the reserve water, accumulated during the night, and held by the translocating system and leaves, plus that continually being added by absorption from the root system, is equalized by diffusion from the leaf. If the water content of the soil is not a limiting

factor, the ability to absorb and translocate very probably becomes so. This would then be a typical "saturation deficit." If this be true, then the maximum to be very high will evidently occur after a very rapid rise, while a less rapid but prevailingly high transpiration rate will utilize the reserve water and reach the limit entailed by anatomical features without having so high an index. There is evidence for support of this in the two curves in question; the average of the indices for the first six hourly readings for July 21 being 0.396, while the average for July 16, computed from the same leaves, for the first six hours preceding the maximum is 0.391, which means that the water loss from a unit area from the first rise in the morning until the attainment of the maximum was practically the same. Granting that the translocating ability limits the maximum rate of transpiration, then, since we are considering data calculated from the same individual with an interval of but five days, we would expect the water loss up to the time of incipient drying to be approximately the same, when the time periods are the same. We may further assume that the water reserve will be quite constant for the same individual on consecutive days when the growth water is adequate to meet all the needs of the plant, for this will be dependent upon the structural features of the plant, which remain quite constant. A slight variation in the reserve would follow a variation in food storage, which is a fluctuating factor, and slight differences in the total transpiration up to the time of the deficit depression will result from different absorption rates which fluctuate with soil temperature. If the transpiration index is high in the morning, the maximum transpiring power will of necessity appear early, for the reserve is utilized rapidly. If the rate is low in the morning, the maximum, if it is attained, will occur relatively late. The maximum transpiring ability is limited by the rapidity of rise in the index and the translocation-absorption ability. The maximum translocation doubtless occurs when the protoplasmic condensation within the mesophyll of the leaf is greatest, since at that time the osmotic pressure within the cells is highest, and the cells will exhibit their greatest affinity for water. This occurs two or three hours after the maximum transpiration. The relatively high transpiration index preceding

the attainment of maximum absorption is possible because of the reserve water which is available in excess of that supplied by the translocation stream.

Curve no. 3, which indicates the transpiration for August 26, shows some features conspicuously unlike those recorded for the two preceding readings. The maximum is lower in this instance than was the minimum index for either of the preceding days. The low amount of growth water, which was only 0.480 per cent at 2.5 dm., was a prominent cause for the lower transpiring power. At 10:00 A.M. visible wilting occurred, and turgidity was not restored within the mesophyll cells of the leaves until about 5:00 P.M. The development of absciss tissue may be considered as contributing to the reduced rate, being earlier at this station than on the open sand, owing to the more frequent production of a wilting coefficient. Evaporation and relative humidity show curves which lie much higher than do those of July 16 and 21. The extremely high evaporation from about 1:30 to 4:30 P.M. was due to high wind velocity.

It will be seen that on different days readings from the same leaves may give widely different results. The three days' readings shown in this instance present different combinations of potent factors, one being a cloudy day with plenty of available water, one a clear day with sufficient growth water, and the third a clear day with low humidity and soil water reduced to the wilting coefficient. Thus the environmental factors which initiate variation in the daily transpiration rate at any given station were found to be the same as those which led to different averages for the various stations. This daily variation is more marked on the sand series than on the clays, although the same phenomena were characteristic of the latter situations. There was found to be more variation in transpiring power between cloudy and clear days than was registered for days when the atmospheric conditions were similar, whether cloudy or clear.

Transpiration on prairie

The transpiration index as recorded for *Tilia* on the prairie indicates that there the species is subjected to a physiological stress in most respects very similar to that found on the dunes (fig. 10).

There is the same tendency on the prairie toward an early rapid rise in the index, and for a maximum which occurs from one to two hours earlier than is characteristic of *Tilia* at the other stations on clay soils. The maximum is relatively very high on the prairie, and is followed quite regularly by a saturation deficit which is more pronounced than that recorded for any other habitat except upon the open dune complex.

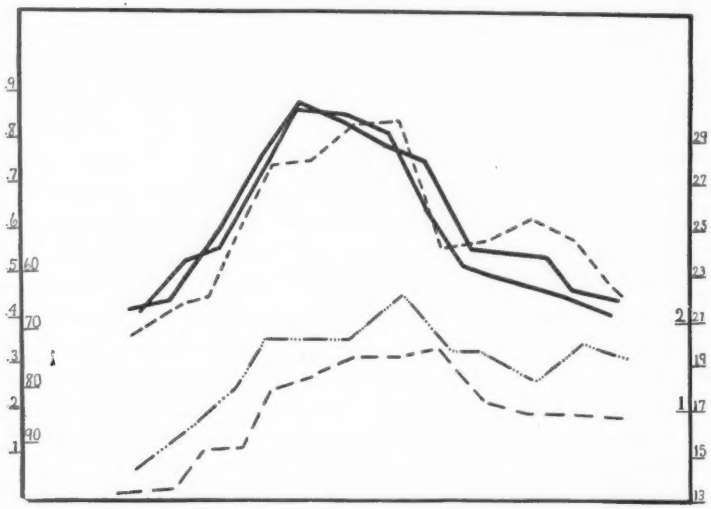

FIG. 10.—Data for station *L* for September 6; note exceptionally high transpiration index characteristic of prairie tension zone; transpiration is great although relative humidity is high and evaporation low.

The prevailing environmental factors show a close similarity to those of the open sands. The growth water is low during much of the summer, the insolation is correspondingly high, the influence of winds is strong and quite constant, prevailing temperatures are higher and are associated with a relative humidity which is low (fig. 10). Thus the features of these two types of associations show remarkable similarity, with the exception of the soil composition and growth water. The growth water falls rapidly during the months of August and September and approaches the dune condition. These factors in conjunction exert an influence which

leads to a high transpiration rate and to the development of morphological features in the leaves which are very similar to those recorded at station *E* on the dunes.

Transpiration in relation to mesophytism

Water content of the soil has long been recognized as a factor which directly influences the climax type of flora that may develop in any given region. The relatively high content as shown for the mesophytic forest has quite generally been ascribed as the reason for the development of the larger thin type of leaf characteristic of that region, in contrast with the smaller more thickened type characterizing open associations. Correlated with this concept frequently has been the idea that transpiration in the mesophytic forest is very high. Observations on the foliar transpiring power of *Tilia* throughout its range of habitats, from the most to the least mesophytic conditions under which it develops, have led to a conclusion in regard to this species which is quite different from that just stated. The greatest transpiring ability was exhibited in the most open situations where the available growth water was least, and the transpiring ability was found to be least in the dense shade of the mesophytic forest and moist ravines where the growth water was relatively very high. It may be asked why the water loss is less in the forest. The question is answered by pointing out that the environmental factors for high transpiration are less potent in the forest than in more exposed positions. Relative humidity is greater, evaporation is less, temperature is lower, light is less intense, soil temperature is lower, and winds are less effective. All of these physical factors combine to give a lower rate of transpiration than occurs in the exposed open situations.

Summary and conclusions

1. The morning rise in the foliar transpiration index for *Tilia* is commonly much slower for the clay series of environments than for the sand dunes, and the maximum attained is comparatively much lower.

2. The time of maximum transpiration is usually from 12:00 to 1:00 P.M. on clay soils, whereas on the sands it occurred from 9:00

to 10:00 A.M. This difference is ascribed to the more rapid utilization of the reserve water which is stored up in the leaves and translocating system of the plant during the night. Thus on the dunes, where the reserve is utilized more rapidly than it is restored by absorption and translocation, there will occur a depression in the index later in the day. On the clay soils, the rise being slower, frequently the reserve is not utilized until midday; hence there occurs a lower maximum and a much less noticeable saturation deficit, or none at all. This means that the maxima of temperature, relative humidity, and evaporation concur in time or more nearly approximate doing so than for the dune series. The closest approximation to this concurrence on the sands was recorded for cloudy days with low temperature and evaporation and a high relative humidity. All these conditions of environment are tendencies toward the prevailing condition in the forest, in contrast with those characterizing open dune situations.

3. The transpiration stream shows a simple curve for readings taken on forested clays, rising gradually to a maximum at noon and falling at approximately the same rate to the night level.

4. The effect of thunder showers is recorded in a sharp reduction in the transpiration index. Frequently when the precipitation occurs in the early afternoon there is a second rise in the transpiration curve to a level in excess of the normal rate for that time, probably owing to the accumulation of a slight reserve, while the transpiration rate is lower than that of absorption.

5. Partial abscission produces an effect not unlike that found accompanying the development of a wilting coefficient. Under these circumstances there is a low morning rise which quite early reaches a maximum, and is followed by a rapid decline accompanied by the closure of stomata and visible wilting, the transpiration falling until it becomes almost entirely cuticular. The morning rise takes place in this instance because of the slight water reserve accumulated during the night.

6. A wilting coefficient did not develop in any of the clay soils, and there was always a considerable amount of growth water available, but its occurrence on the sand series produced an effect closely similar to that occasioned by abscission.

7. Sunlight affects the transpiration stream through its influence in initiating stomatal movements, and has particular reference to the morning rise. Direct sunlight accelerates the water loss, due apparently to a rise in temperature of the mesophyll cells which would be followed by a greater molecular diffusion of water from the cell walls into the lacunae of the leaf, thus increasing the diffusion gradient.

8. Relative humidity is a very potent factor in influencing the transpiration index. By increasing or decreasing, it affects directly the diffusion gradient between the external and internal atmospheres. Sudden changes in this factor almost invariably affected the transpiration stream, even when the atmometer failed to register it. When the relative humidity is great there seldom is any saturation deficit developed, but when it is low and the evaporation rate increases greatly the reserve will probably be consumed and a saturation deficit will follow. Relative humidity is considered a very potent factor leading to such depression in the curve.

9. Growth water exerted less influence in modifying the transpiration rate than did most of the atmospheric factors. There is little evidence that it is a potent factor at all on the clay series. Its direct effect is most noticeable when it approximates the wilting coefficient as was recorded on the sand dunes, when the index is observed to fall rapidly. The growth water was always more than could be utilized in the clay environments, and hence never proved a limiting factor.

10. The part played by soil temperature in maintaining the transpiration stream is considered more important than has generally been ascribed to this factor. The close parallel of the soil temperature and transpiration curves is strongly indicative of its influence (fig. 7), and especially is this significant since there is strong evidence that the absorption rate often becomes a limiting factor. I believe that since soil temperature bears a direct relation to absorption it will eventually be found to be of great significance in limiting the foliar transpiring ability.

11. The highest average transpiring power recorded for the clays, with the exception of the prairie data, was that registered for the swamp habitat. In this environment *Tilia*, while producing

a relatively high water loss as on the dunes, is growing in the very opposite environment in reference to its physical factors. The growth water and relative humidity are greater here than at any other station, while soil temperature, evaporation, and atmospheric temperature are lowest. Of these factors, measured soil moisture might be cited as the causal factor leading to increased transpiration, but it seems improbable that this factor can be responsible for the higher water loss. It is more probably associated with structural features, the correlation of root and leaf development, or the greater exposure to light.

12. The variation in average transpiring power from day to day as recorded for the same leaves is greater for the mesophytic forest than is the difference between the average rates for the most mesophytic and most xerophytic stations, if we consider the clay series only and disregard the prairie record. The converse is true for the dune series.

13. Daily variations in the transpiration stream are most pronounced in the xerophytic situations, and least so in the strongly mesophytic ones.

14. The average transpiring power is less in deep forests and moist ravines than in open woodlands, and less in open forests than in exposed positions on clay. The greatest transpiring ability was recorded on the open sands where there was no humus, and on the prairie.

15. The transpiration curve characteristic of the prairie station is closely similar in its essential features to the curves representing the open dune sands. There is a more rapid morning rise as compared with the forest, owing to the greater light exposure at that period, a tendency to an earlier maximum due to a greater water reserve, a more frequent recurrence of a saturation deficit, and finally a steeper afternoon decline than is commonly recorded for the clay environments.

16. The highest transpiration rates are found to be associated with a low growth water, which is not interpreted as being in any way causal, but as evidence that growth water is of relatively little significance so far as transpiration is concerned until it approaches the wilting coefficient.

17. High mesophytism leads to low transpiration in *Tilia*, and large leaves of thin texture transpire at slower rates than do smaller leaves which are more leathery and resistant in nature.

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THE VESSEL IN SEED PLANTS[1]

MARY C. BLISS

(WITH PLATES XVI–XX)

In view of the recent discussion of the evolution of the vessel in Gnetales and Angiosperms by THOMPSON (**5**), it was suggested to the writer that a comparative study of the vessel in seed plants would be of interest in bringing forward more evidence which might have weight for or against the theory that the presence of vessels in these two groups is an argument for genetic relationship. The discussion of scalariform pitting in the secondary wood of Angiosperms by BROWN (**2**) also suggested the larger question of the origin of the vessel in seed plants, that is, has it been derived from the pitted tracheids of the more primitive plants, or is the scalariform vessel the more primitive, from which the pitted vessel has been derived?

By way of introduction I wish to discuss briefly the vessel of *Pteris aquilina* as an example of the lower vascular plants. The side wall, usually at a definite angle with the end wall, is marked with scalariform bordered pits (fig. 1, right). The borders are very clearly evident in the profile view of the vessel (fig. 4). The typical end wall of the vessel is characterized by scalariform perforations in which the border has wholly disappeared at the center, but is still visible at both ends of the perforation (fig. 3). The difference between the openings in the side and end walls is again very clearly seen in the profile view of the vessel (fig. 4). The border has practically disappeared from the perforation, although occasionally it is evident near the juncture of the end wall with the side wall. Another striking difference in the perforations of side and end walls is the reaction to stains. The end wall gives a definite cellulose reaction with haematoxylin, while in the side wall blue is present only in the middle lamella and the pit membrane, the border of the perforation taking a definite lignin stain with

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

safranin. This difference separates very distinctly the side and end walls when viewed under the microscope. An interesting condition is seen in fig. 1, where the end wall at the center is perforated by a series of bordered pits which gradually grade into scalariform pits and perforations at the lower end of the figure. Fig. 2 shows an end wall which is clearly reticulated, a stage intermediate between the typical scalariform perforation and the more unusual pitted type. It is interesting to note in this connection that in the higher groups of the Filicales (Osmundaceae and Ophioglossaceae) the side wall of the vessel is likewise pitted and not scalariform as in most ferns. These observations as seen in figs. 1 and 2 give weight to the view that the end wall is the more specialized portion of the vessel and more advanced in its organization, and that in the pitted end wall of *Pteris* we have the forerunner of the pitted type of perforation characteristic of the lateral walls of the element in the higher groups.

Gnetales

Turning now to the vessels of the seed plants, we may consider first the vessels of Gnetales. The vessels in the young twig of *Ephedra* (fig. 5) show perforations which are clearly bordered pits. Although the torus has entirely disappeared and the border is very much reduced in nearly all of the pits, the torus is present in two of the pits in the upper portion of the vessel at the right. Fig. 6 shows larger vessels of an older twig, the vessel at the right being more advanced than the vessel at the left. Here the perforation consists of a series of bordered pits in which the membrane has entirely disappeared. Since the end wall of the vessel is the most specialized, it would naturally show the greatest advance in development, and this is true in the higher types of Gnetales. In radial sections of the stem of the *Gnetum Gnemon* type (figs. 7, 8) all stages are found, from the clustered bordered pits of the *Ephedra* type to the open pore of the higher forms, and transitional fusion perforations are clearly seen (fig. 7). The mature stem of the *Gnetum Gnemon* type is illustrated in fig. 9, where the vessels are characterized by the typical porous perforations of the higher forms. In contrast with the *Gnetum Gnemon* type, *Gnetum scandens*, an advanced vine species of the genus, is interesting.

While the vessels of this type in the mature secondary wood of the stem are also characterized by the large bordered open pores, a consideration of the primitive regions, such as the primary wood and the wood of the leaf trace, shows that the open pore has been derived from pit fusions. Fig. 10 illustrates a radial section of the stem of *Gnetum scandens* cut directly through the primary wood. A protoxylem element with its spiral markings is visible just at the left of the vessel. At the lower part of the figure the pits are quite distinct, suggesting the *Ephedra* type, but in the center the fusion is practically complete. In the leaf trace of *Gnetum scandens* (figs. 11, 13) is a condition similar to the perforation found in the older twig of *Ephedra*, showing the scalariform pits obviously the result of the fusion of bordered pits. A higher magnification of a similar perforation is shown in fig. 12, bringing out more clearly the borders of the pits. Thus in *Gnetum scandens* we do not find always the fusion of pits haphazardly arranged as THOMPSON (5) describes for *Gnetum*, but fusion of pits side by side (figs. 12, 13), a condition which, as shown later, is paralleled in the fusion of pits in the vessels of Angiosperms.

Welwitschia shows the open bordered pore type of perforation in the vessel of the mature wood (fig. 14). The border of the pit is clearly visible in the vessel to the left, while in the vessel to the right the edge of the perforation faces the observer. The vessel of the leaf trace in *Welwitschia* (fig. 15) shows the more primitive type of vessel as found in *Ephedra*. Thus the monotypic genus *Welwitschia* illustrates the same general principles shown for *Gnetum*, namely, that in the vessel wall of primitive regions is found the *Ephedra*-like type of vessel with pitted perforation. It may be added that *Welwitschia* and *Gnetum* are usually distinguished from *Ephedra* by absence of the torus in the bordered pit.

Angiosperms

Liriodendron and *Magnolia* may be considered as representatives of a possibly primitive group of Angiosperms, the Magnoliaceae. In the side wall of the vessel is the same general principle illustrated in the end wall of the Gnetales. Fig. 16 shows vessels in the mature secondary wood of a small twig of *Liriodendron Tulipifera*. Here

the vessels, both the lateral wall and the perforations, are obviously scalariform. This situation has recently been emphasized by BROWN (2) as showing the derivation of the vessel of Angiosperms from the scalariform tracheid. The condition found in the primitive regions of *Liriodendron*, however, particularly the primary wood of the root, by no means seems to justify this conclusion. Fig. 17 shows a radial section in the region of the primary wood of the root of *Liriodendron Tulipifera*. All three vessels are characterized by pitted lateral walls and not by scalariform sculpture. A higher magnification of a portion of the vessel seen at the extreme right is shown in fig. 18. The center of the vessel exhibits scalariform perforations. It is equally clear that this scalariform perforation passes gradually into pits both above and below. Fig. 19 shows the perforation above and the lateral wall of the vessel below, with the gradual transitions from pits to perforations particularly clear. The perforations show the so-called "ghosts" of former pits, which become more and more pitlike as one passes downward, until the typical bordered pits become clearly recognizable. Still another illustration of the same phenomenon is seen in fig. 20. It is clear from these illustrations that in *Liriodendron Tulipifera* there is a gradual transition from pits to scalariform perforations in the vessels of the primary wood.

It is evident that the perforations of the vessels in Filicales and Gnetales represent the most advanced condition of the vessel wall. The obvious interpretation, as seen in *Liriodendron*, is that the side wall represents the primitive pitted condition, while the perforation has been derived from the fusion of pits precisely as in *Gnetum* and *Welwitschia*. The seriation of events cannot possibly be regarded as reversible, for if that were the case, we should have to regard the perforation as representing the primitive condition of the vessel wall, a position which is untenable.

Magnolia Frazeri has a greater tendency to scalariform perforations and lateral pitting than the other species of the genus which have been observed. As in *Liriodendron*, the most interesting condition here is found in the region of the primary wood of the root. Fig. 21 shows a radial section through this region. The perforation in the center gradually grades into pits above and below,

a condition practically identical with a similar section of the root of *Liriodendron* as seen in fig. 18. Fig. 22 illustrates the character of the vessel in the first annual ring of a branch of *Magnolia Frazeri*. The perforation is obviously scalariform, while the lateral wall is characterized by typical pits. The end wall perforations again show evidence of fusion of pits in the "ghosts" and indentations on the scalariform openings. In many instances scalariform perforations may be seen to grade into pits in the wood of the stem of *Magnolia Frazeri*. It seems clear from a study of the primary wood region of the root of *Liriodendron* and *Magnolia* that the vessel with pitted walls is antecedent to the vessel with scalariform walls, and further that the scalariform perforations which are universal in the vessels of *Liriodendron Tulipifera* and are likewise found frequently in the vessels of species of *Magnolia* are the result of fusions of pits precisely as in the case of the perforations of the vessels of *Gnetum* and *Welwitschia* in Gnetales. Since evidence from primitive regions in Gnetales has been used by THOMPSON (**6**) in tracing the origin of the perforations in vessels of that group, the validity of a similar procedure as regards the evidence in the Magnoliaceae obviously must be admitted.

As another representative of the Ranales, the ranunculaceous genus *Paeonia* is interesting as showing in the vessels of the stem typical scalariform perforations (fig. 23). This observation confirms SOLEREDER'S (**4**) statement that "only simple perforations have been observed in the woody and herbaceous genera of this group with the single exception of *Paeonia*." In the leaf trace of a species of *Paeonia* (figs. 24, 25) in the region of the primary wood, the perforations show the more primitive pitted condition combined more or less with the more modern scalariform condition. The protoxylem elements are visible at the left of the figures, and here again in close proximity to the primary wood (fig. 25) we have the vessel with the pitted side wall.

The Betulaceae, a group of the Angiosperms often regarded as primitive, is of importance in regard to the evolution of the angiospermous vessel as compared with the origin of the vessel in Gnetales. THOMPSON (**5**) concludes that the mode of origin of vessels in the two groups is quite different. Moreover, he states

that "since the Gnetalean vessel usually has only two rows of circular pits, no matter how the fusions take place no scalariform bars can result." It has already been seen that in *Gnetum scandens* (figs. 12, 13) the scalariform perforations are very evidently the result of fusion of opposite circular pits. Further evidence of such progression in the evolution of the perforation is seen in the Betulaceae. The typical end wall of the vessel in this group is scalariform. Such an end wall is seen in the stem wood of *Betula alba* in radial aspect in fig. 28. In this type of scalariform end wall there is usually no indication of the derivation of the scalariform perforation from fusion of pits, although instances of this condition are not infrequent even in the mature wood. It is the vessels which lie near the primary wood which are of greatest interest from an evolutionary standpoint. Fig. 26 shows three such vessels, the spiral elements of the protoxylem lying to the left of them. The vessel nearest the protoxylem has a perforation which is intermediate between scalariform and pitted, this condition being most clearly recognizable at the middle of the figure. In the vessel next to the right the transitions appear only at the top and bottom of the perforation, while in the third vessel the fusion of pits is practically complete. Haphazard fusion is evident in the lower portion of the perforation. Fig. 27 illustrates another vessel taken from a different preparation, in which the perforation is much less extensive than in the preceding figure, and the derivation of the scalariform perforation from pit fusions at the top and bottom is particularly clear.

The same conditions which have been noted for *Betula* are found also in *Alnus*. The typical end wall of the vessel is scalariform, as seen in fig. 31. Practically no indication of pit fusions is seen, but fig. 29 is evidence that such fusion has taken place. In the lower part of the figure more or less haphazard fusion is evident, while in the upper region two elongated pits are still distinct. A higher magnification of the same end wall is seen in fig. 30. It is clear for the Betulaceae as exemplified by *Betula* and *Alnus*, as for the Magnoliaceae, that the scalariform perforation as shown by primitive regions is derived from pit fusions and does not represent the persistence of a primitive scalariform condition of the vessel wall.

Passing to a consideration of a type of vessel in the Angiosperms which is characterized by porous and not scalariform perforations, and taking a form nearly allied to the Betulaceae, *Quercus velutina*, we invariably find in the mature wood porous perforations which in the smaller vessels sometimes show a border like that characteristic of similar perforations in *Gnetum*. SOLEREDER (4) has already pointed out in the oak and other representatives of the Fagaceae that scalariform perforations are characteristic of regions near the primary wood. I have been able to confirm this general statement of SOLEREDER in regard to the oak. A radial section of *Quercus velutina* (fig. 32) through the primary wood of the leaf trace shows a very interesting condition in the perforation. The transition from the pitted to the scalariform condition is very clear. Usually the perforations of the vessels in the primitive region of *Quercus* are scalariform only, without transition from the pitted condition. In *Fagus* one frequently finds vessels with scalariform perforations even in the mature wood.

We may now consider the Rosaceae, a higher group, characterized in general by porous perforations of the vessels. Taking first a herbaceous representative of the family, fig. 33 shows a vessel in the region of the primary wood of the stem of *Potentilla monspeliensis*, an annual herb. The vessels in this region have scalariform perforations which pass gradually, by the disappearance of transverse bars, into porous perforations. SOLEREDER has described a similar condition in *Potentilla fruticosa*, and it appears to be widespread in the genus. As a woody representative of the group, *Cydonia* is interesting as showing the scalariform perforation of the vessel in the region of the primary wood (fig. 34), as found in *Potentilla*. An interesting situation is presented by the organization of the vessel in the primitive region of the leaf trace, in its course in the stem of *Cydonia japonica* (fig. 35), in which the perforation is pitted, a very significant condition. Taking the Rosaceae as illustrated by *Potentilla* and *Cydonia*, it seems clear that the porous condition of the perforation has been preceded by the scalariform, and the scalariform in turn by the pitted.

In the Vitaceae the lateral walls of the vessels in contact with other vessels are practically universally scalariform. This condition is of particular interest because the scalariform lateral sculpture of vessels is a phenomenon of rare occurrence in most angiospermous orders, being usually confined to a single genus and occasionally to a single species. If we examine the primitive region of the stem near the primary wood, vessels with pitted lateral walls may often be found (fig. 37). A further fact which has some bearing on the situation is the occurrence of pits on those walls of the vessels which are in contact with the vasicentric parenchyma, characteristic of this group. This situation is not the less striking because ray cells and even longitudinal parenchymatous elements in the Angiosperms in general are frequently related to vessels by means of fusion pits of a scalariform nature. This condition is widespread among the Angiosperms. It has been pointed out by BAILEY (1) in this connection that in modern species of *Pinus* the lateral pits of the rays often undergo fusions. Similar conditions are often found in the Podocarpineae, Taxodineae, and Cupressineae, and has even been found in Paleozoic Gymnosperms. Fig. 38, illustrating the same section as fig. 37, farther out from the primary wood, shows the type of vessel characteristic of the mature wood of the Vitaceae as a group, with scalariform sculpture. It is apparently quite clear that the vessel with scalariform lateral pits in the Vitaceae has been derived from a pitted predecessor, and that it is not a primitive vessel type in this family.

Turning now to the perforation of the vessels in the Vitaceae in the mature wood of *Leea* and *Vitis*, the vessels are characterized by large open terminal pores. This confirms SOLEREDER's statement that the vessels in the Vitaceae "have simple circular or elliptical perforations." Such a perforation is seen in the radial section of the stem of a species of *Leea* in the region of the primary wood (fig. 36) at the right of the figure. A very interesting fusion scalariform perforation is seen in the vessel on the left. The photograph in this case is not clear, owing to the thickness of the section, but seen under the microscope it is an unusually vivid demonstration of the course of events in the evolution of the open

pore. Fig. 39 shows vessels from the leaf trace of *Vitis* in its course in the stem. On the left in the region of the primary wood two vessels show scalariform perforations; to the right is the single open pore typical of the vessels of the group. An interesting reversion to the primitive type of perforation in this genus is seen in the radial section at the end of the annual ring (fig. 40). The spring vessels show the open pore characteristic of the mature wood, but in the summer wood, which is in some respects a primitive region, we have the reversion to the scalariform type of perforation characteristic of the regions of the primary wood and of the leaf trace. From the evidence given it seems clear that in the Dicotyledons as in the Gnetales the scalariform perforations have arisen by the fusion of pits, and that this fusion may be haphazard or serial.

Conclusions

This investigation covers the origin of the vessel in *Pteris*, in Gnetales, and in dicotyledonous Angiosperms. In *Pteris* the primitive condition of the vessel is scalariform, with the obvious tendency to the development of pitted sculpture in the end wall of the element. It is of interest to note that in the Osmundaceae and Ophioglossaceae the pitted as contrasted with the scalariform sculpture appears in the side walls of the vascular elements.

In Gnetales the vessels have obviously been derived from pitted and not from scalariform tracheids. Their evolution is connected with the appearance of particularly large pits in the end walls of the vascular elements, which first lose their membranes and subsequently undergo fusions, either transversely or irregularly. As in *Pteris*, it is the perforation region of the vessel which shows the greatest advance and specialization. In the Dicotyledons two general types of vessels are found, those with scalariform perforations and those with porous perforations. Investigation of the first type from the Magnoliaceae and Betulaceae appears to establish the fact that the perforations have arisen by pit fusions precisely as in the higher Gnetales. In the second type the vessel with porous perforation, often with bordered margins as in *Gnetum*, in most cases in the Angiosperms has had its immediate origin from the vessel with scalariform perforations. These in turn, as illus-

trated by *Quercus* and *Cydonia*, have been derived from the fusion of pitted perforations. It follows that the mode of origin of the vessel in the Dicotyledons and Gnetales is essentially similar, in both cases being the consequence of the fusion of open bordered pits, either in rows or irregularly.

These remarks apply to the end wall of the vessel, particularly to the perforation. In the few cases among the Angiosperms where the lateral vascular walls are scalariform, it appears clear that the scalariform lateral pits have resulted from the horizontal fusion of circular or oval pits. It is further to be noted that the scalariform sculpture appears first in the terminal region of the vessel and may later appear in the side wall, always resulting from pit fusions. It follows that the vessel of the Angiosperms as of the Gnetales has been derived not from the scalariform but from the pitted tracheid. In this respect the vessel is in harmony with the other evolutionary developments in the wood, since according to the best established view both the mechanical fibers and the longitudinal parenchymatous elements of higher plants have been derived from the pitted tracheid (3). It would be surprising if the vessel, which is much later in geological times than longitudinal storage elements and mechanical elements of strength, should have originated from a type more primitive than the pitted tracheid.

Summary

1. In *Pteris* the scalariform perforation of the vascular end wall often becomes pitted.

2. In the *Gnetum* type of vessel the fusion of pits to form the porous perforation is haphazard, but in *Gnetum scandens* the fusion of pits is often more regular, resulting in a scalariform perforation.

3. Haphazard fusion of pits is also found in *Paeonia*, *Cydonia*, and *Leea;* while in *Liriodendron*, *Magnolia*, *Paeonia*, *Betula*, *Alnus*, *Quercus*, and *Vitis* the fusion is often serial, resulting in scalariform perforations.

4. The evolution of the perforations of the vessels in Gnetales and Dicotyledons is similar, and in both cases is the result of pit fusions.

5. From evidence derived from a consideration of primitive and conservative regions in *Liriodendron*, *Magnolia*, *Paeonia*, and *Vitis*, it may be concluded that the primitive type of vessel in the Angiosperms is pitted, and has been derived from the pitted tracheid as have the mechanical and longitudinal storage elements of the wood.

This investigation has been carried on in the laboratories of plant morphology at Harvard University under the direction of Dr. E. C. JEFFREY. In conclusion I wish to express my thanks to him for the material supplied and for his invaluable aid throughout the work.

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EXPLANATION OF PLATES XVI–XX

PLATE XVI

FIG. 1.—Longitudinal radial section of bundle of rhizome of *Pteris aquilina;* ×250.

FIG. 2.—End wall of vessel of *Pteris aquilina* in face view, reticulated type; ×250.

FIG. 3.—End wall of vessel of *Pteris aquilina* in face view, scalariform type; ×250.

FIG. 4.—Portion of vessel of *Pteris aquilina*, profile view; ×166.

FIG. 5.—Longitudinal radial section of young twig of *Ephedra;* ×125.

FIG. 6.—Longitudinal radial section of older twig of *Ephedra;* ×250.

FIG. 7.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×62.

FIG. 8.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×187.

PLATE XVII

FIG. 9.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×250.

FIG. 10.—Longitudinal radial section of stem of *Gnetum scandens* in region of primary wood; ×250.

FIG. 11.—Longitudinal radial section of leaf trace of *Gnetum scandens;* ×40.

FIG. 12.—Longitudinal radial section of leaf trace of *Gnetum scandens* showing end wall; ×250.

FIG. 13.—Longitudinal radial section of leaf trace of *Gnetum scandens;* ×125.

FIG. 14.—Longitudinal radial section of mature wood of *Welwitschia mirabilis;* ×250.

FIG. 15.—Longitudinal radial section of leaf trace of *Welwitschia mirabilis;* ×250.

FIG. 16.—Longitudinal radial section of mature secondary wood of small twig of *Liriodendron Tulipifera;* ×250.

PLATE XVIII

FIG. 17.—Longitudinal radial section of root of *Liriodendron Tulipifera* in region of primary wood; ×187.

FIGS. 18–20.—Longitudinal radial section of root of *Liriodendron Tulipifera* in region of primary wood; ×250.

FIG. 21.—Longitudinal radial section of root of *Magnolia Frazeri* in region of primary wood; ×250.

FIG. 22.—Longitudinal radial section of first annual ring in stem of *Magnolia Frazeri;* ×250.

FIG. 23.—Longitudinal radial section of stem of *Paeonia moutan;* ×125.

FIG. 24.—Longitudinal radial section of leaf trace of species of *Paeonia;* ×250.

PLATE XIX

FIG. 25.—Longitudinal radial section of leaf trace in species of *Paeonia;* ×250.

FIG. 26.—Longitudinal radial section of stem of *Betula alba* in region of primary wood; ×250.

FIG. 27.—Longitudinal radial section of vessel of *Betula alba* in region of primary wood; ×375.

FIG. 28.—Longitudinal radial section of secondary wood of *Betula alba;* ×250.

FIG. 29.—Longitudinal radial section of stem of *Alnus incana* in region of primary wood; ×250.

FIG. 30.—Same as fig. 29; ×375.

FIG. 31.—Longitudinal radial section of secondary wood of *Alnus incana;* ×375.

FIG. 32.—Longitudinal radial section of leaf trace of *Quercus velutina* in region of primary wood; ×375.

PLATE XX

FIG. 33.—Longitudinal radial section of stem of *Potentilla monspeliensis* in region of primary wood; ×250.

FIG. 34.—Longitudinal radial section of stem of *Cydonia vulgaris* in region of primary wood; ×250.

FIG. 35.—Longitudinal radial section of leaf trace of *Cydonia japonica;* ×250.

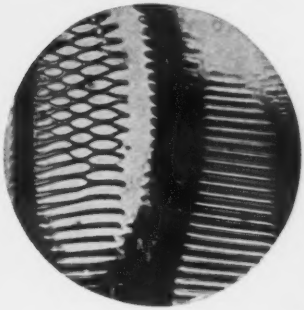
FIG. 36.—Longitudinal radial section of stem of species of *Leea* in region of primary wood; ×250.

FIG. 37.—Longitudinal radial section of stem of species of *Vitis* in region of primary wood; ×250.

FIG. 38.—Same as fig. 37, farther out from primary wood; ×250.

FIG. 39.—Longitudinal radial section of leaf trace of species of *Vitis;* ×250.

FIG. 40.—Longitudinal radial section of spring and summer wood in species of *Vitis;* ×250.



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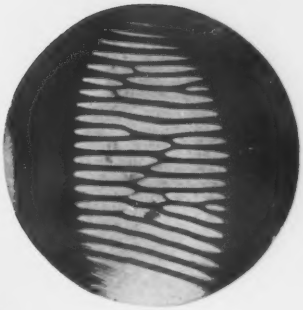

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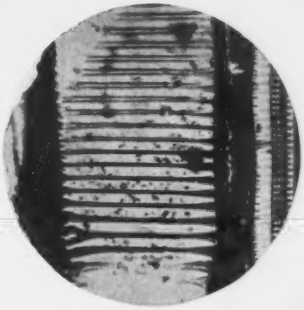

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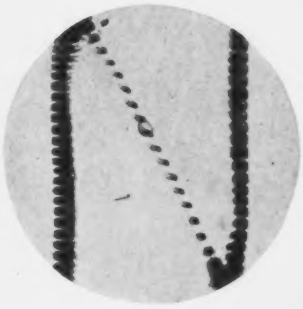

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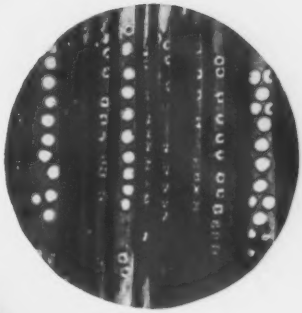

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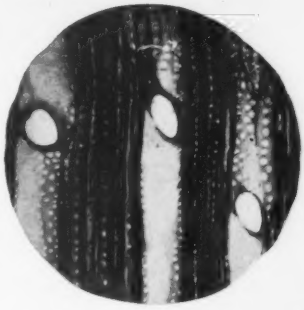
BLISS on VESSEL IN SEED PLANTS



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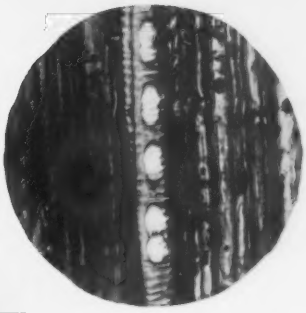

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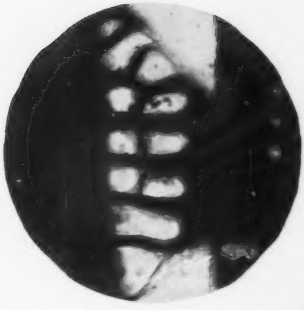

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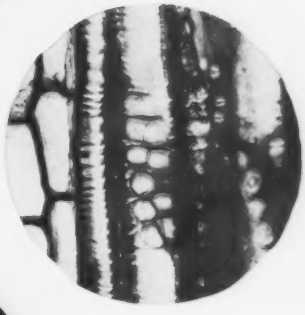

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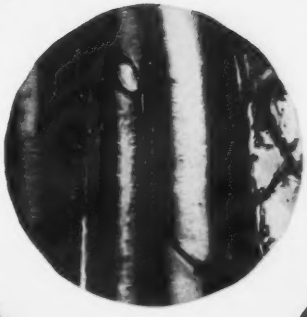

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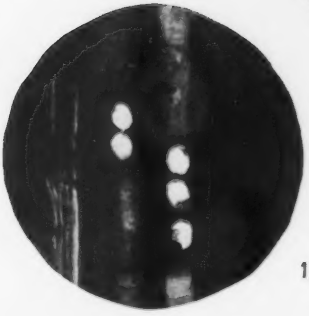

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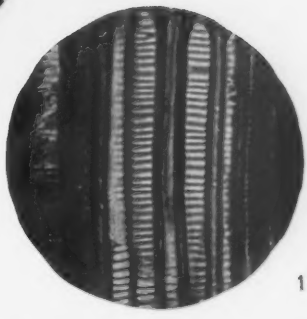

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BLISS on VESSEL IN SEED PLANTS

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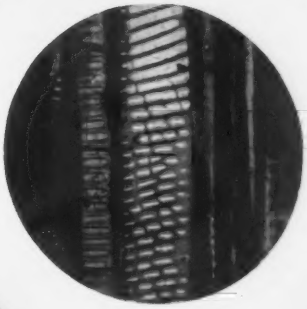

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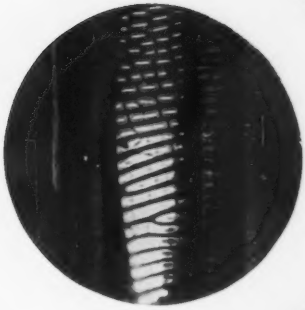

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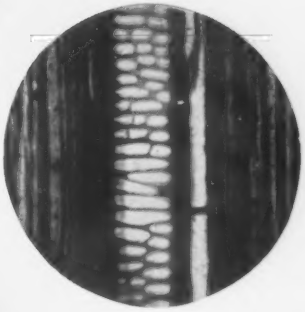

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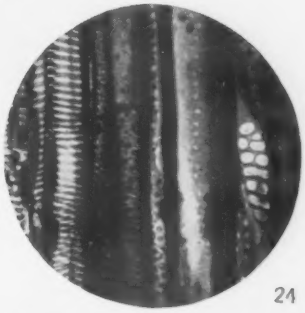

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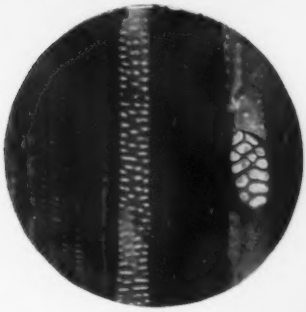

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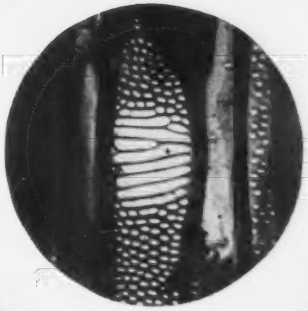

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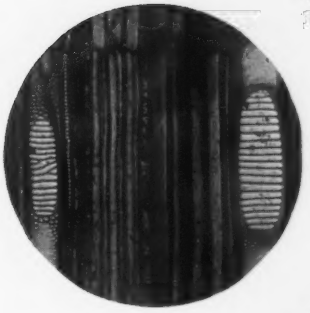

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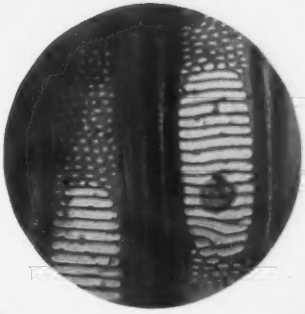

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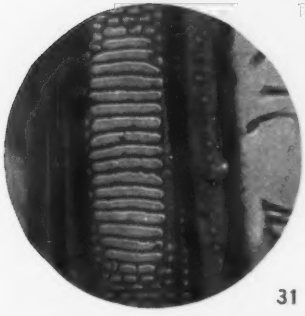

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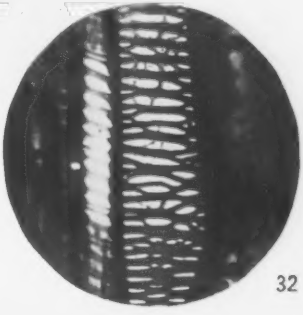

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BLISS on VESSEL IN SEED PLANTS

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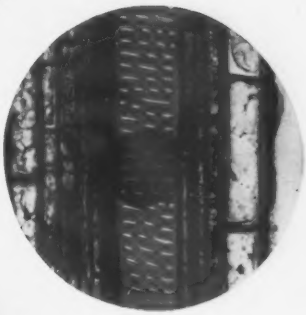

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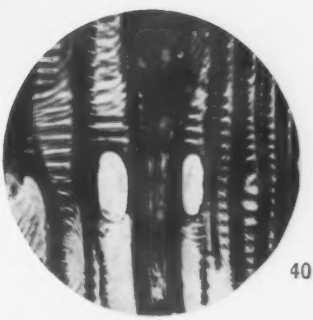

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BLISS on VESSEL IN SEED PLANTS

A CONVENIENT THERMOREGULATOR

HEINRICH HASSELBRING

(WITH TWO FIGURES)

A convenient form of thermoregulator which has now been in use in several laboratories of the Bureau of Plant Industry, United States Department of Agriculture, for nearly ten years is shown in fig. 1. On account of its compactness and its adaptability to constant temperature baths and chambers of various kinds, where extreme sensitiveness is required, it may perhaps be worth while to give a brief description of the instrument and its installation in order to make it more generally available.

The instrument consists of a thermometer tube about 30 cm. long, the upper end of which is bent over and enlarged into a bulb to serve as a reservoir for excess mercury. The thermometer bulb at the bottom should be about 7 or 8 cm. long. Platinum contacts leading to the binding posts clamped on the thermometer are sealed into the capillary at *A* and *B*. At a point (*C*) some distance from the upper contact a slight constriction is formed in the thermometer capillary. This point may be marked on the tube. For ordinary incubator temperatures the constriction should be about 2.5 cm. above the upper contact; for temperatures around zero it should be 5 or 6 cm. above.

Experience with many of these instruments has shown that in their manufacture the observance of several points is absolutely essential. (1) The space above the mercury must be entirely free from gas. The presence of a trace of gas prevents the union of mercury from the reservoir with that of the capillary and makes the instrument entirely useless. (2) The platinum wires must project far enough into the capillary to make contact with the mercury, but not so far that they interfere with the motion of the mercury column. If the wire projects too far into the capillary

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the mercury will hang on the wire, and regulation thereby becomes impossible. The seal must be gas-tight. (3) The constriction of the capillary at *C* must be narrow enough so that a short section of the mercury column above will not slide down past the constriction even with slight jarring. It must be possible, however, to shake mercury down past the constriction. (4) The band holding the upper contact wire should not cover the contact point itself, otherwise adjustment is difficult.

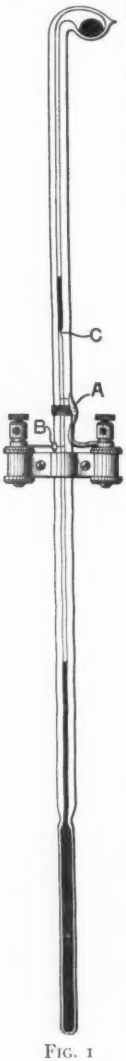

FIG. 1

To adjust the instrument for a given temperature an excess of mercury is shaken down below the constriction to unite with the column in the capillary. The remainder of the mercury above the constriction is allowed to flow, with gentle tapping or shaking, if necessary, into the upper bulb, the thermometer being inclined during the process. The constriction should be narrow enough to prevent the mercury below from flowing past it. The bulb of the regulator is now plunged into a large beaker of water kept exactly at the temperature for which the regulator is to be set. The mercury column will stand a little above the upper contact, since an excess of mercury was first shaken down past the constriction. The length of the mercury column above the contact is noted, and a section of nearly the same length is forced above the constriction by carefully lowering the bulb into another vessel of water kept at a sufficiently higher temperature. The bulb is then replaced in the first vessel and the process repeated. Finally, only single globules are forced past the constriction until the end of the column stands exactly at the upper contact wire, when the bulb is kept in water at the desired temperature. If the constriction has been properly made, the short piece of mercury column above it may be left in place.

This regulator is designed to actuate a telegraphic relay which interrupts the heating current. The installation shown in fig. 2

requires but little explanation. The current passing through the regulator and actuating the relay may be taken either from a line circuit or from a constant circuit battery. In either case the current should be so reduced by means of resistance and by reduction of the voltage that the current passing through the regulator does not exceed 0.015 of an ampere. Larger currents damage the regulator. Various types of heaters may be used, but in general the current to be interrupted by the relay should be as small as possible. Where high temperatures are to be maintained, it is usually best to have an auxiliary heater which by running con-

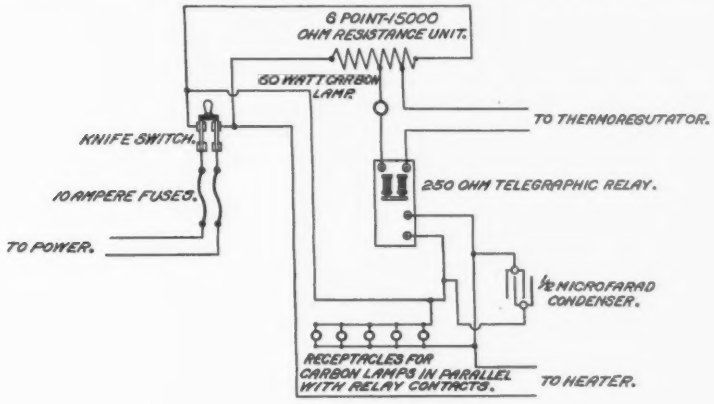

FIG. 2

stantly maintains the temperature nearly at the desired point. The deficiency is controlled by a heater of smaller capacity regulated by the relay. If only one heater is employed, a large portion of the current may be made to flow continuously by inserting one or a number of carbon lamps in the circuit in parallel with the relay. The sparking at the relay contacts is thus greatly reduced. It is scarcely necessary to state that the relay magnets, armature spring, and contact points of the relay should be adjusted very carefully. When all adjustments of the installation are perfect, there is practically no spark at the relay contacts when the heating current is interrupted, and a barely audible click of the armature. With proper installation, ordinary telegraphic relays of 250 ohms' resistance will break a current of 2 amperes with practically no spark at

the contacts. For larger currents it is better to use some form of solenoid control switch actuated by the relay.

The installation shown in fig. 2 is adapted for a direct current circuit. In this case the current for the relay magnets is taken from the line as shown. If alternating current only is available, the current for actuating the relay should be supplied by a suitable constant circuit battery. Dry cells may be used if the current is on only for comparatively short intervals. In either case the current should not exceed 0.015 of an ampere. If an alternating current is used in the heating circuit, the condenser is not necessary, the reduction of the spark in that case being effected by the lamps alone.

The regulators were constructed by HENRY J. GREEN, of Brooklyn, New York, to whom I am indebted for interest and cooperation in perfecting the instrument.

BUREAU OF PLANT INDUSTRY
WASHINGTON, D.C.

BRIEFER ARTICLES

WILLIAM HARRIS

(WITH PORTRAIT)

WILLIAM HARRIS was born November 15, 1860, at Enniskillen on Lough Erie, in County Fermanagh, northern Ireland, and was of Scotch descent. In 1881 he went to Jamaica, and left there for the first time in September 1920, when he came to the United States to receive medical treatment for an inflammation of the esophagus. He died at the home of his elder son in Kansas City, Missouri, on October 11, 1920.

After receiving his earlier education from tutors at home, and spending some months at Cowan's Nurseries, Liverpool, at the age of eighteen Mr. HARRIS went to the Royal Botanic Gardens at Kew to study botany and gardening. Before he was twenty-one he was appointed from Kew to be superintendent in the Botanical Department of Jamaica. In 1899 the value of his botanical work was recognized by his election to the Linnaean Society of London. In 1908 he became Superintendent of Public Gardens and Plantations in Jamaica, and in 1917 was made Government Botanist. In April 1920 he was appointed Assistant Director of Agriculture, retaining also the office of Government Botanist. In his several official positions he showed a high degree of administrative ability. He possessed not only the capacity for looking after essential details in carrying out plans, but had also the imagination necessary for planning new projects. During the war Mr. HARRIS served with untiring energy as secretary to the Advisory Board on Food Production.

Mr. HARRIS was a naturalist from boyhood. This was perhaps to be expected of one whose father was devoted to plants and gardening, and whose youth was spent amid the lakes and rugged hills about his birthplace. Throughout his life, in spite of many administrative duties, he remained an ardent and keenly observant field naturalist. Although his interest was primarily in plants, it also embraced animals. The writer, for example, recalls participating in a rather exciting chase of a 4 ft. iguana, which seemed ignominiously ended with the big lizard ensconced in a narrow mouthed pocket in a limestone ledge, but Mr. HARRIS volunteered to seize the ugly jawed creature by the neck and so to pull

it from its retreat. The animal was thus captured without being mutilated, and later became a much prized specimen of the United States National Museum. A similar enthusiasm, coupled in this case with marked endurance, was shown by the more than 100 monthly trips made over the rough mountain trails from Cinchona to Blue Mountain peak, to secure records of the climatic peculiarities of this highest elevation in Jamaica. These records are probably the only ones yet made at any such elevation (7428 ft.) in the West Indies, or for that matter in all eastern North America. During these trips, as on his official journeys to other parts of the island, he persistently observed and collected the native plants.

The chief contributions to botanical science made by Mr. HARRIS were those to plant taxonomy and floristic geography. While the herbarium at Hope Gardens (it was at Cinchona until 1897) was under his care, that is, from 1908 to 1920, as well as for two previous decades while under the supervision of the Director of Agriculture, the Honorable William Fawcett, thousands of specimens were added to it, collected chiefly by Mr. Harris himself. These plants were gathered not only during his official trips to various parts of the island, but also while on special expeditions to the less settled parts of Jamaica. Thus he accompanied expeditions sent by the New York Botanical Garden to the "Cockpit country" of central Jamaica in 1906; one to the Santa Cruz Mountains in 1907; around the whole coast and to the Blue Mountains in 1908; and one to the John Crow Mountains of eastern Jamaica in 1909. Dr. BRITTON, in recalling these expeditions, pays this tribute to HARRIS as a coworker: "He was one of the most enjoyable scientific companions I have ever known, always cheerful, active, and original." Of the 8000 Jamaican species added to the herbarium at Hope during the 29 years

it was under the care of Mr. HARRIS, several dozens were new to science, while scores or probably hundreds were of species known elsewhere but hitherto unreported in Jamaica. Because of this wide experience in the field, coupled with his remarkably retentive memory of the appearance of any plant that he had once seen, he probably knew the characters and distribution of the vascular plants of Jamaica more thoroughly than they had been known by any earlier botanist. The herbarium built up under his care is perhaps the most important in the West Indies.

The publications of Mr. HARRIS include several considerable pamphlets published separately and numerous briefer articles and reports in the Bulletin of the Botanical Department of Jamaica. Most of these were on the economic and ornamental plants of the island. It is fitting that his services to botany should be commemorated in the names of the plants he discovered. This is done by the generic names *Harrisia* (Cactaceae) and *Harrisiella* (Orchidaceae), as well as by the specific names *Harrisii* or *Harrisiana* given to a score or so of ferns and seed plants, which will serve to remind future botanists of the part he played in West Indian botany.

It is due to the alertness and initiative of Mr. HARRIS that the Cinchona Tropical Station has been open to American botanists during the past 18 years. On each of the several occasions when Cinchona seemed likely to be diverted from the botanical service for which it is so eminently fitted, it was he who made the first move toward insuring its continuance as a botanical station. All American botanists who have worked in Jamaica have a very warm appreciation of the keenly intelligent assistance rendered them by Mr. HARRIS on every occasion. Those of us who may be fortunate enough to work in Jamaica again will miss his courteous and resourceful aid. Most of all will we miss his cordial welcome to the hospitality of Hope Gardens and the stimulating contact with an enthusiastic naturalist and an altogether delightful man.—D. S. JOHNSON, *The Johns Hopkins University, Baltimore, Md.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Ecological classification.—In a moderate discussion of the classification of vegetation, TANSLEY[1] has clarified some obscure points and made several good suggestions. He insists that it is absolutely necessary to consider the units of vegetation as they actually occur in nature, and not to attempt to classify vegetation either by life forms or habitats. The natural units of vegetation to be employed in any system of classification in the first instance must be determined empirically. These units are essentially topographical units, and are to be grouped according to development. While differing in many ways from true organisms, they may most conveniently and most correctly be regarded as quasi-organisms. In this respect the author takes what appears to be a safe stand midway between such extreme views as those of CLEMENTS, who regards vegetational units as true organisms, and those of GLEASON, who refuses to consider a unit of vegetation as an organic entity. The plant "association" is regarded as the primary and fundamental unit of vegetation. In this TANSLEY is in agreement with a majority of ecological investigators, although he lays great stress upon the limitation of the term to mature units in relatively stable equilibrium with their environment. Transitory plant communities are differentiated from fully developed ones, and are termed "associes." For parts of associations and associes dominated by a single species, it is suggested that CLEMENT's usage be followed by designating them respectively "consociations" and "consocies."

The continued use of "formation" is recommended. The formation must be determined empirically, and it consists of a set of plant communities related developmentally and culminating in one or more associations. It is regarded as possible to distinguish climatic and physiographic (edaphic) formations, although not so sharply as has been done by NICHOLS, because of the frequent replacement of climatic by physiographic factors which is gradual in the transition region between two climatic regions. It is recommended that plant associations be named by their dominant species, and the formations, whenever it is possible to do so, from the form of the vegetation.—GEO. D. FULLER.

Anatomy of Equisetum.—Several recent papers help considerably to settle the controversy over the fundamental nature of the bundles and the stele in *Equisetum*. MEYER[2] presents a detailed review of the vascular anatomy of

[1] TANSLEY, A. G., The classification of vegetation and the concept of development. Jour. Ecol. **8**: 118–149. 1920.

[2] MEYER, F. J., Das Leitungssystem von *Equisetum arvense*. Jahrb. Wiss. Bot. **59**: 263–286. *figs.* 7. 1920.

one species, paying particular attention to the node. Miss BARRATT[3] treats several species in a thorough manner, especially the anatomy of sporelings. Lady ISABEL BROWN[4] is continuing her painstaking studies of the anatomy of the cone, adding two more species to those now known in detail. She has also[5] given her attention more fully to the broader aspect of the comparative morphology. These students of *Equisetum* all present convincing evidence of great reduction in the vascular tissues. All are of the opinion that the internodal ring of vascular bundles represents a more extensive and continuous mass in ancestral forms, and believe the three separated xylem strands of each bundle to be the remains of one continuous strand, except that Miss BARRATT considers the protoxylem is always an independent strand. The phylogenetic unity of the individual bundle in *Equisetum* seems well established. Leaf gaps do not exist; the gaps in the cone stele have no morphological value. Nodes and internodes do not exist in the cone, and the sporangiophores are organs *sui generis*. No true secondary growth occurs at the nodal ring.—I. W. BAILEY.

Ecology.—Although one of the youngest members in the group of biological sciences, ecology in America has already passed two conspicuous milestones of progress. The first was the establishment in 1915 of the Ecological Society of America, which now has a membership of over 350, and usually supplements its annual meeting in December with a summer gathering upon the Pacific Coast. The appearance during 1920 of the four numbers constituting the first volume of a journal[6] devoted entirely to the interest of ecologists marks the passing of the second milestone.

The purpose of the new journal is well expressed in the "foreword" contained in the first number: "This journal is issued to meet the demand for the collective publication of articles on ecology. Its pages are open to all who have material of ecological interest from whatever field of biology. While the variety of fields may cause diversity of treatment, yet the ecological significance of the papers will make them of general interest. Specialization is inevitable, but makes more urgent the need for cooperation. To approach different subjects from similar points of view is to lay the foundation of cooperation." An examination of the first volume shows that all phases of the subject are being cared for. This is evidenced by the inclusion of 10 articles dealing with the more general aspects or including a discussion of both plants and animals, while an equal number deal rather exclusively with plants and six

[3] BARRATT, KATE, A contribution to our knowledge of the vascular system of the genus *Equisetum*. Ann. Botany **34**: 173–200. *pls. 6, 7. figs. 24.* 1920.

[4] BROWN, ISABEL M. P., A third contribution to our knowledge of the anatomy of the cone and fertile stem of *Equisetum*. Ann. Botany **34**: 237–263. *pls. 8, 9. figs. 7.* 1920.

[5] ———, Phylogenetic considerations on the internodal vascular strands of *Equisetum*. New Phytol. **19**: 11–25. *figs. 7.* 1920.

[6] Ecology (continuing the Plant World). Quarterly Journal. BARRINGTON MOORE, editor; Brooklyn Botanic Garden, publisher. **1**: pp. 313. 1920.

articles relate to animal ecology. The new journal compares favorably in general appearance and typography with the *Plant World*, which it replaces, and seems likely to reflect credit upon its editor, with his associated editorial board, as well as upon the Ecological Society of America.—GEO. D. FULLER.

Marine algae of Beaufort.—HOYT[7] has published a very full account of the marine algae of the region adjacent to the biological station of the Bureau of Fisheries at Beaufort, N.C. The ecological data are fully covered in a general description of the region, the variation in the floras of different parts of it, the conditions of temperature, light, salt content of water, turbidity, water movements, and habitats, and finally the regional, seasonal, vertical, and horizontal distribution of algae. Methods for collecting and preserving algae are given, and also some account of their economic uses. In the classification and description of the algae of the region, 128 species are included, distributed as follows: Myxophyceae 10, Chlorophyceae 23, Phaeophyceae 25, and Rhodophyceae 70. An artificial key to genera and a full bibliography are also provided.

The Bureau of Fisheries is to be commended for such a publication. It feels called upon to give the following explanation: "The question may be asked, Why should the Bureau of Fisheries be interested in marine algae? Excluding purely scientific considerations, there may be recalled the well known fact that all animals depend on plants for food, and this is as true of water animals as of land animals."—J. M. C.

Ecology of algae.—In the sandhill region of western Nebraska are numerous small lakes, all comparatively shallow, and varying much in alkalinity. ANDERSEN and WALKER[8] have studied the algal vegetation of several of these and endeavored to measure the controlling factors. They found the means available for measuring light were entirely insufficient and resulted in nothing but the crudest approximations. The mineral and gas content of the water, however, showed a direct relation to the algal flora. A rather definite seasonable periodicity was manifest, and in the extensive lists of species this relationship is indicated.—GEO. D. FULLER.

Montane plants of the southern Rockies.—Continuing his studies of the flora of the Rockies, RYDBERG[9] has analyzed the plant population of the southern portion of the range. The formations distinguished are the pine forest, spruce forest, aspen and poplar groves, alder-willow swamps, copses, and sage brush. Lists of species are given for each formation.—GEO. D. FULLER.

[7] Hoyt, W. D., Marine algae of Beaufort, N.C., and adjacent regions. Bull. Bur. Fisheries **36**:371–556. *pls. 84–119.* 1920.

[8] ANDERSEN, EMMA N., and WALKER, ELDA R., An ecological study of the algae of some sandhill lakes. Trans. Amer. Micr. Soc. **39**:51–85. *pls. 3–12. fig. 1.* 1920.

[9] RYDBERG, P. A., Phytogeographical notes on the Rocky Mountain region. IX. Wooded formations of the mountain zone of the Southern Rockies. Bull. Torr. Bot. Club. **47**:441–455. 1920.

NEW BOOKS

The "University of Chicago Italian Series" edited by ERNEST H. WILKINS, Professor of Romance Languages in the University of Chicago. This series is to consist of a grammar, a reader, and editions of modern Italian novels, plays, and other works. There have already been published

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Farina's *Fra le corde d'un contrabasso*, edited with Notes and Vocabulary by ELSIE SCHOBINGER and ETHEL PRESTON. $1.40, postpaid $1.50.

The Press and Politics in Japan. By KISABURŌ KAWABÉ. $2.00, postpaid $2.15. The purpose of this book is to show the influence of the press upon the political life of Japan. It is an orderly arrangement of the significant facts of a rapidly developing civilization and furnishes the student of ancient and modern Japan with an abundance of information regarding the rapid transformation which has taken place since 1868. It will therefore be interesting reading, not only to the students of sociology, but also to those who are interested in journalism, politics, and history.

Principles of Accounting. By ALBERT C. HODGE and JAMES O. MCKINSEY, the School of Commerce and Administration, the University of Chicago. $3.00, postpaid $3.15. This book fills the special need of a beginning text in accounting to prepare the student for business. The discussion of principles of accounting is primarily in terms of the function of accounting as an administrative aid to the business manager. Consideration is given to the forms of reports and records and the classification of accounts.

Proceedings of the National Conference of Social Work, 1920. $3.50, postpaid $3.65. The publications of this organization are written by specialists, men and women who are authorities in their various branches of social improvement. They discuss problems and practical methods, and seek to disseminate information helpful to the social worker.

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